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Developmental Selection Against Developmentally Unstable Offspring and Sexual Selection

ANDERS PAPE MØLLER*

Laboratoire d'Ecologie, CNRS URA 258, *Université Pierre et Marie Curie, Bât. A, 7ème étage, 7 quai St. Bernard, Case* 237, *F*-75252 *Paris Cedex* 05, *France*

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Gametes and offspring are often produced in excessive numbers, and developmental selection against early developmental stages reduces the number of offspring to what can be safely reared. Developmental selection is hypothesized to act mainly against gametes or zygotes with developmentally deviant phenotypes, and surviving offspring will hence give rise to adults with a developmentally more stable phenotype. This hypothesis is supported by observations of unsuccessful gametes or offspring often having developmentally deviant phenotypes or genetic characteristics such as chromosomal aberrations that give rise to developmental instability. Developmental selection against developmentally unstable offspring is furthermore suggested to be a direct outcome of sexual selection often being related to developmental stability. Sexual selection for developmentally stable mates is suggested to result in production of developmentally stable offspring, if a general developmental program gives rise to developmental stability both among adults and among gametes and subsequent offspring.

1. Introduction

Reproduction and survival are the two main components contributing to fitness. The reproductive component is affected by the trade-off between quality and quantity of offspring. Parents therefore have to optimize reproduction. However, parents often produce many more offspring than they can possibly rear in order to be able to produce a sufficient number of successful offspring (Mock & Forbes, 1995). Such parental "optimism" may be beneficial for two different reasons. First, it may facilitate production of the optimal number of offspring even in the face of errors such as the inability of some eggs to hatch. Second, parents may chose to invest in the available offspring, but only a small number of superior quality offspring will receive full investment (Kozlowski & Stearns, 1989).

*E-mail: amoller@hall.snv.jussieu.fr

The observation that parents often invest in a small proportion of initiated offspring gave rise to the selection-arena hypothesis. This hypothesis suggests that a range of reproductive phenomena such as incompatibility systems, pollen selection, sperm selection, and selective abortion represent an integrated genetic sieve favouring the genotypes that are most likely to make the greatest contributions to maternal fitness (Bertin, 1982; Stephenson & Bertin, 1983; Eberhard, 1985; Stearns, 1987). The excess number of initated gametes and embryos thus represents what is subsequently discarded by parents when chosing among the potential candidates for rearing and full parental investment. Evidence consistent with the selection-arena hypothesis is positive genotypic correlations of fitness between individuals of different ages as demonstrated in some studies (Mulcahy *et al*., 1975; McKenna & Mulcahy, 1983; Norris, 1994; Petrie, 1994).

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A useful general term for selective episodes related to discrimination among more and less fit gametes and offspring is developmental selection (Buchholz, 1922). This was initially suggested to occur when plants (or other organisms) preferentially reared outcrossed offspring in favour of self-fertilized offspring of poorer quality (Buchholz, 1922). However, developmental selection may be applied to a greater range of phenomena related to parental selection of offspring of variable genetic or phenotypic quality.

The main hypothesis presented in this paper is that developmental selection often acts against offspring of low phenotypic quality because they are developmentally unstable. Developmental stability reflects the ability of organisms to undergo stable developmental under a range of different environmental conditions (Ludwig, 1932; Palmer & Strobeck, 1986; Parsons, 1990; Møller & Swaddle, 1997). Developmental instability is measured as random deviations from an optimal phenotype, for example, in terms of fluctuating asymmetry or phenodeviance. A range of environmental and genetic stresses have been shown to result in increased developmental instability of the morphology of phenotypes [Ludwig, 1932; Palmer & Strobeck, 1986; Parsons, 1990; review in Møller & Swaddle (1997)]. However, developmental instability has also been suggested to be reflected in deviant physiology, immunology, and behaviour (Zakharov, 1992). Developmental instability is traditionally assumed to be related to poor performance in terms of energetics, growth and fitness (Palmer & Strobeck, 1986), and a recent review of the literature provides extensive support for this assumption (Møller & Swaddle, 1997). The first hypothesis presented here is that generally developmental selection can be considered to select against developmentally unstable phenotypes both at the gamete and the embryo levels. The second hypothesis is that sexual selection often acts in favour of developmentally stable individuals as shown by a large number of observational and experimental studies [reviews in Møller (1993), Watson & Thornhill (1994), Møller & Swaddle (1997)]. If a common developmental program results in development of a stable phenotype at different stages of the life-cycle, then sexual selection in favour of developmentally stable partners will simultaneously be developmental selection against developmentally deviant offspring. These hypotheses differ from the selection-arena hypothesis by emphasizing the role of developmental processes in developmental selection, and by providing a link between developmental selection and sexual selection.

2. Developmental Stability of Successful Gametes and Offspring

DEVELOPMENTAL SELECTION AGAINST DEVELOPMENTALLY UNSTABLE GAMETES

Sperm are often produced in excess numbers in relation to the number needed for fertilization of eggs. This excess production of sperm has been explained in terms of sperm competition by which sperm from different males compete by numbers for access to a limited number of eggs (Parker, 1970). Cohen (1969, 1973; see also Manning & Chamberlain, 1994) suggested that the production of large numbers of sperm was a consequence of many sperm being abnormal in phenotype due to production errors. This idea can be directly related to developmental selection against gametes with developmentally unstable phenotypes. Sperm production rates are negatively related to a range of environmental and genetic stress factors (Romanoff, 1960; Sheldon, 1994). Exactly the same factors that are known to increase the level of developmental instability in general morphology of organisms [reviews in Palmer & Strobeck (1986), Parsons (1990), Møller (1996), Møller & Swaddle (1997)] also decrease the quality of sperm [inbreeding (Wildt *et al*., 1987; O'Brien, 1994), environmental factors such as malnutrition (Romanoff, 1960), pesticides and other pollutants (Henderson *et al*., 1986; Harrison & Boer, 1977), temperature (VanDemark & Free, 1970), and parasites and diseases (Romanoff, 1960; Harrison & Boer, 1977)]. It is tempting to speculate that sperm which do not fertilize eggs have developmentally unstable phenotypes, and that this is the causal reason for the inferiority of their success. Although it is generally believed that sperm phenotypes are under the control of the parental genotype (Parker & Begon, 1993), the mechanism of developmental selection against deviant gametes could work under both haploid and diploid genetic control of phenotypic expression. Mainly morphologically normal sperm may reach the site of fertilization or the site of sperm storage (Birkhead *et al*., 1993). If this is the case, then Cohen's idea of production errors being the main cause of gamete redundancy is to some extent supported. Selection at the embryo stage against deviant phenotypes may further reduce the success of genetically dysfunctional sperm.

Sperm are not the only gametes that are produced in excess numbers. For example, female mammals generally produce many more eggs than will ever fully develop. This is the case in humans in which many more eggs are available than will ever be fertilized (Simpson *et al*., 1982). Several mammals

have polyovulation such as pronghorn antelope *Antilocapra americana* and plains viscacha *Lagostomus maximus* although only a smaller number of eggs will ever become implanted (Birney & Baird, 1985; Stearns, 1987). Polyovulation in mammals and the production of excess ova may have a similar explanation as the production of excess sperm (Birney & Baird, 1985). Only a small number of eggs will ever develop, and, although direct evidence is absent, I hypothesize that eggs of inferior quality in terms of phenotype may be selected against. The extent to which selection will act against developmentally unstable eggs remains unexplored.

DEVELOPMENTAL SELECTION AGAINST DEVELOPMENTALLY UNSTABLE OFFSPRING

Studies of developmental selection involving offspring are much more common than studies involving gametes. Many studies of plants demonstrate developmental selection (Mulcahy, 1979; Stephenson, 1981; Stephenson & Bertin, 1983; Willson & Burley, 1983; Bawa & Webb, 1984; Charlesworth *et al*., 1987; Wiens *et al*., 1987; Lee, 1988; Lyons *et al*., 1989; Marshall & Folsom, 1991; Searcy & Macnair, 1993). Plants appear to select developmentally against offspring sired by pollen bearing the less valuable genotype (Searcy & Macnair, 1993). Developmental selection often acts against inbreeding, which is known to increase the level of developmental instability [reviews in Palmer & Strobeck (1986), Parsons (1990), Møller & Swaddle (1997)]. Marginally self-fertilized offspring may be reared only when too few outcrossed offspring are formed (Cheplick, 1992). This evidence for developmental selection against developmentally deviant gametes is extremely weak and does not allow any firm conclusions.

Fruit or seed abortion provides an opportunity to cull offspring on the basis of the quality of their genotypes (Lloyd, 1980). Seed abortion may enhance seedling quality by abortion of inferior seeds with poor phenotypic or genetic qualities (Stephenson, 1981; Bawa & Webb, 1984; Lee, 1988). Undamaged juvenile fruits abscise because of genetic or developmental abnormalities (Kraus, 1915; Bradbury, 1929; Sarvas, 1962; Sweet, 1973; Stephenson, 1981). When fruit loss is determined by the maternal sporophyte, the remaining progeny tend to show higher seed set and greater seed viability than when an equivalent number of randomly chosen fruit is removed (Stephenson & Winsor, 1986). This situation has been described by Haig (1990) in an ESS model on the optimal allocation of a sporophyte's resources among seeds, when the seeds differ in expected fitness. The fitness gain per unit of investment is maximized when all seeds falling below a certain minimum threshold are aborted and the rest provisioned. Whether particular seeds are aborted depends on information on the particular seed. If only the presence of embryos can be recorded by the sporophyte, then only seeds with embryos should be provided. More detailed information on the relative viability of embryos as determined for example by developmental stability would lead to more fine-tuned strategies.

Plants differ widely in their progeny to zygote ratios due to extensive embryo abortion (Wiens *et al*., 1987). Interspecific variation in the frequency of embryo abortion appears to be related to the degree of outcrossing. Frequencies of developmentally unstable embryos in plants such as *Epilobium angustifolium* may exceed 70%, and these high frequencies are caused by developmental errors during the early stages of embryogenesis (Wiens *et al*., 1987). Aborted embryos are fertilized as evidenced from the presence of a pollen tube and/or necrotic tissue. There is clear evidence of developmental instability among aborted embryos as determined from (1) irregular divisions in the suspensor or the embryo proper, (2) highly vacuolated and necrosed cells, (3) malformed cotyledons, and (4) a tilted position of the embryo or a movement of the embryo toward the chalazal end (Wiens *et al*., 1987).

When environmental stress is more prevalent, developmental selection is more intense (Zamir *et al*., 1982; Zamir & Gadish, 1987; Mulinix & Iezzoni, 1988; Marshall & Whittaker, 1989; Sari-Gorla *et al*., 1989; Searcy & Macnair, 1990). This may indicate that stress directly influences the phenotype of pollen and hence their fertilization ability. It is known for developmental stability of morphology that a range of stresses increases the level of fluctuating asymmetry and the frequency of phenodeviants (e.g. Palmer & Strobeck, 1986; Parsons, 1990; Møller & Swaddle, 1997). Differences in fitness produced by selfing or out-crossing can increase with stress (Dudash, 1990), and increased levels of stress result in elevated levels of developmental instability. Postzygotic developmental selection is often more important under stressful environmental conditions (Searcy & Macnair, 1993; Marshall & Ellstrand, 1988; Marshall, 1988; Ellstrand & Devlin, 1989).

The literature on developmental selection in animals is much more restricted than the plant literature. However, it is unlikely that this reflects a real difference in the relative frequency of developmental selection simply because there is an old tradition of studies of developmental selection among botanists. Since the responses of animals to

developmentally unstable offspring can be directly assessed, it is relatively easier to determine the target of selection. One of the most clear examples of developmental selection against developmentally unstable offspring concerns the scorpion *Pandinus imperator* (Mahsberg, 1996). Females of this species provide extensive parental care, and newly born offspring must climb to the cephalothorax of the mother in order to obtain protection. Any offspring with morphological malformations that are unable to climb to the cephalothorax as newborns are eaten by the mother. Such malformed offspring are relatively common, and when reared in isolation together with offspring of normal phenotypes, they still remain malformed with poor reproductive and survival performance when becoming adults. Hence, maternal developmental selection against developmentally unstable offspring does not result in wastage of parental investment in offspring of poor quality.

Malformations are commonly reported among social insects, but the behaviour of adults toward such individuals remains unknown. Injured ants or broods, which may be considered to be individuals with deviant phenotypes, are sometimes killed and eaten by the adult nest-mates, especially when a wound releases hemolymph (B. Hölldobler, pers. comm.).

In hemi- and holometabolous insects malformed individuals are rarely encountered because such malformation generally will result in an inability to eclose.

Developmental selection against developmentally unstable offspring has with the exception of mammals rarely been reported among vertebrates. In the blue peacock *Pavo cristatus* hatching failure is positively related to the amount of fluctuating asymmetry in ocelli of the train feathers of the sire (M. Petrie, pers. comm.). This correlation implies that a measure of developmental instability among adults reliably reflects the developmental ability of offspring in the subsequent generation.

Developmental selection has been described in some detail in mammals. Among house mice *Mus musculus* mothers eat the placenta and the umbilical cord until they reach the belly of the offspring. Healthy pups then begin to squeak and the mother stops eating and starts licking the pup (Ehret & Bernecker, 1986). Pups that fail to cry will be killed and eaten (Ehret, 1975; B. König, pers. comm.). Offspring with major abnormalities are rare, but clearly belong to this category of offspring with abnormal behaviour. It is common knowledge among researchers studying mice that abnormal offspring are routinely eaten, although detailed quantitative information is absent (B. König pers. comm.).

There is an extensive literature on human abortion and infanticide related to developmental instability. In humans a large fraction of all spontaneous abortions have abnormal karyotypes, including polyploids (Simpson *et al*., 1982; Boue *et al*., 1975; Wolf *et al*., 1984). Abnormal karyotypes are also associated with elevated levels of fluctuating asymmetry and frequencies of various phenodeviants [review in Møller & Swaddle (1997)]. A sample of human abortuses had a high frequency of dermatoglyphic phenodeviants compared with the prevailing postnatal condition in the population (Babler, 1978). Mutants and immunologically defective embryos are identified early in development and discarded as abortions (Diamond, 1987; Stearns, 1987; Uyenoyama, 1988). Malformation frequency and prenatal mortality rise with time between ovulation and insemination, suggesting that aging effects of gametes also may play a role (Guerrero, 1974; Guerrero & Rojas, 1975; Harlap, 1979). Deviations from optimal phenotypes in terms of immunology can account for early stage abortion of MHC homozygotes that are known to have reduced parasite resistance (Beer & Quebbeman, 1982). The proximate mechanism generating abortion in humans appears to be low levels of secretion of human chorionic gonadotropin, which binds to the mothers' luteinizing hormone receptors and stimulates the release of progesterone, a menstruation blocker (Haig, 1993).

Developmental selection against developmentally unstable phenotypes also takes place by means of infanticide. In human societies both physical and mental deformities are common reasons for infanticide (Ford, 1964; Montag & Montag, 1979). An analysis of data in the Human Relations Area Files reported killing or abandonment of deformed or very ill children at birth in 21 of 35 societies (Daly & Wilson, 1984). Such children would have trouble surviving in primitive societies with limited resource access even if attempts were made to keep them alive.

Hybridization may also lead to developmentally unstable offspring with high levels of morphological abnormalities and resultant poor survival prospects. For example, this is the case for fertilized eggs and embryos of hybrids between the frogs *Litoria ewingi* and *L. paraewingi* (Watson *et al*., 1971; Watson, 1972). Similarly, hybrid offspring from crosses of fire-bellied toads of the species *Bombina bombina* and *B. variegata* have a high frequency of developmental anomalies. These include tooth row deformations that may impair feeding and vertebral anomalies (Szymura & Barton, 1986). Hybrids between sunfishes displayed similarly high frequencies of morphological

abnormalities (Whitt *et al*., 1977). It is likely that such abnormal offspring have poor survival prospects and therefore contribute to maintenance of hybrid zones.

3. Sexual Selection and Developmental Selection

Sexual selection arises as a result of the advantages that some individuals have over others of the same sex and species in exclusive relation to reproduction (Darwin, 1871). Both competition among individuals of the chosen sex (usually males) for access to the other sex and choice of partners by individuals of the choosy sex (usually females) may give rise to sexual selection [reviews in Darwin (1871) and Andersson (1994)]. Choosy individuals may obtain either direct or indirect benefits from their mate choice (Andersson, 1994; Møller, 1994). Direct benefits include resources such as nuptial gifts, territories, and paternal care, while indirect fitness benefits include genetically attractive traits for sons and general viability for offspring of both sexes. Females appear to pay attention to developmental stability of secondary sexual characters (Møller, 1990, 1992). A large number of observational and experimental studies has now provided evidence for the generality of this phenomenon [reviews in Møller (1993) and Watson & Thornhill (1994)]. Females may, from choice of males with developmentally stable phenotypes, obtain mates that are better able to provide parental care, that have more attractive phenotypes, or that father offspring with developmentally superior phenotypes (Møller, 1993). A female preference for males with developmentally stable phenotypes may result in developmental selection, if a general developmental program affects the expression of phenotypes at different stages of the life cycle (Møller, 1995b). This hypothesis resembles the suggestion by Trivers (1985) that females should tend to choose mates that particularly benefit daughters. If male secondary sexual characters are costly, female preferences will evolve to favour males whose expression of the secondary sexual trait confers low fitness on males, but high fitness on females (Seger & Trivers, 1986; Trivers, 1985, 1988). This phenomenon is not well-studied and only two potential examples are available.

Pollinators often have a preference for developmentally stable, symmetrical flowers (Møller & Eriksson, 1995; Møller, 1995a). The proximate mechanism causing this preference appears to be visual acuity toward floral symmetry, probably due to the production of higher pollinator rewards in developmentally stable flowers (Møller & Eriksson, 1995; Møller, 1995a). In *Epilobium angustifolium* there is a clear preference by pollinators for bilaterally symmetrical flowers, as determined from observations and experiments (Møller & Eriksson, 1995; Møller, 1995a). Embryo abortion is extensive in this outcrossing plant with often more than 70% of the embryos being aborted (Wiens *et al*., 1987). A cross-pollination experiment revealed that the abortion rate was strongly negatively related to the level of developmental stability in the flower of both the pollen donor and the pollen recipient (Møller, 1995b). The mate preference for symmetrical flowers as mediated by pollinators therefore resulted in the production of a larger number of developmentally stable embryos.

Females of the blue peacock prefer males with the most elaborate train in terms of size and symmetry (M. Hiraiwa-Hasegawa, pers. comm.). In blue peacocks hatching failure is positively related to fluctuating asymmetry in ocelli of the train of the sire (M. Petrie, pers. comm.). Female peacocks that chose mates with symmetrical ocelli will therefore benefit by hatching a larger fraction of their eggs.

Further tests of whether choice of developmentally stable mates results in the production of developmentally stable offspring is needed.

4. Discussion

This paper presents two related ideas on how developmental stability may be related to developmental selection either in terms of direct selection against developmentally unstable offspring or indirectly in terms of choice of mates with a genetically based, general program for developmental stability. There are several pieces of information consistent with the first mechanism of developmental selection against developmentally unstable gametes or embryos. Particularly, many of the environmental and genetic factors resulting in elevated intensities of developmental selection are also known to give rise to elevated levels of developmental instability. Developmental selection against unstable gametes and embryos may not be comparable for several reasons. Stearns (1987) suggested that selection of sperm and pollen is less reliable than selection of embryos for three reasons: (1) offspring fitness depends on complementarity of gene combinations in the diploid state, and selection based on haploid gametes thus will only provide a less reliable means of improving the quality of offspring. (2) Sperm and pollen phenotypes do not or only to a small extent reveal their genotypes because of the predominant paternal effects. The extent to which gametes signal their

haploid genotype is a controversial issue, although the current state of knowledge appears to suggest a preponderance of genes of parental origin being expressed (Parker & Begon, 1993). This fact may favour developmental selection against developmentally unstable phenotypes, if the same genes for developmental stability are expressed in gametes and diploid life stages. (3) If males are the homogametic sex, sperm selection cannot be used to adjust sex ratio. This latter issue may be relatively unimportant compared with the importance of production of viable, developmentally stable offspring.

The second mechanism that can generate developmental selection against developmentally unstable offspring is by means of sexual selection. If sexual selection in terms of female choice or male-male competition generally favours individuals with high degrees of developmental stability, as suggested by a review of the current evidence (Møller, 1993), this may have consequences for the phenotypes of offspring. A review of the literature on the quantitative genetics of developmental stability revealed an overall highly significant heritability (Møller & Thornhill, 1997). This result was independent of whether studies were based on parent–offspring regression analyses, sib analyses, or selection experiments (Møller & Thornhill, 1997). The ability to generate a developmentally stable phenotype at different stages of the life cycle may have a common genetic background. This assumption is supported by the observation that developmental stability of offspring, as reflected by embryo abortion in *Epilobium angustifolium*, is positively correlated with fluctuating asymmetry in flowers of both the pollen donor and the pollen recipient (Møller, 1995b). Individuals of the choosy sex that mate with a developmentally stable partner will tend to produce developmentally stable offspring under these conditions. This mechanism of mate choice is consistent with the idea that females during their mate choice tend to favour features of the phenotype of males that will benefit daughters over sons (Trivers, 1985, 1988; Seger & Trivers, 1986).

A very large number of loci with small phenotypic effects is likely to be responsible for the developmental program resulting in the development of a stable phenotype. Substantial additive genetic variance in developmental stability may therefore be maintained even in the presence of intense directional developmental selection against developmentally unstable phenotypes.

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