Etología, 3:199-208 (1993)

Developmental stability, sexual selection, and the evolution of secondary sexual characters

A.P. Møller

Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden, Tel.: (+46) 18 18 26 40, Fax.: (+46) 18 55 98 88, E-mail: ZOOAM@SEUDAC21

ABSTRACT. *Developmental stability, sexual selection, and the evolution of secondary sexual characters*.- Developmental stability is hypothesized to play an important role in sexual selection because of the relationship between individual genetic quality and developmental stability and because performance generally is reduced with increasing levels of various measures of developmental instability. I briefly describe (i) the relationship between prevailing mode of selection and developmental stability; (ii) the relationship between sexual selection and developmental stability; (iii) assessment of developmental stability in sexual selection contexts; and (iv) fitness benefits accrueing to individuals that discriminate against mates with a high level of developmental instability.

KEY WORDS. Developmental stability, Fluctuating asymmetry, Mate choice, Sexual selection, Signalling

Introduction

Sexual selection was proposed by Darwin (1871) to arise from the advantages that some individuals have over others of the same sex and species entirely in relation to reproduction. Sexual selection could account for the evolution and the maintenance of extravagant secondary sexual characters such as antlers, horns and spurs used in the context of competition between individuals of one sex for access to individuals of the other and characters such as extravagant plumes, vocalizations and pheromones associated with mate choice.

Students of sexual selection have traditionally only measured one side of bilaterally symmetrical morphological characters used in sexual signalling. In 1990 I suggested that females may assess developmental stability of male secondary sexual characters during their choice of mates because the level of developmental stability would reliably reflect the general health of mates (Møller, 1990). This hypothesis has since been extended (Møller & Pomiankowski, 1993a) and received a considerable amount of empirical and theoretical attention (e. g. Ridley, 1992).

Most organisms are radially or bilaterally symmetrical, but morphological characters usually demonstrate small, random deviations from the optimal phenotype of perfect symmetry which is termed fluctuating asymmetry (FA) (reviews in Ludwig, 1932; Palmer & Strobeck, 1986; Parsons, 1990). These deviations from perfect symmetry are caused by an inability of the individual to control development and result from a wide range of environmental (e. g. food deficiency, pollutants, parasites, diseases) and genetic stress (e. g. homozygosity, inbreeding, hybridization) (reviews in Palmer & Strobeck, 1986; Parsons, 1990). Conspecifics and heterospecifics can potentially use the level of FA as a reliable health certificate of the individual because it is very difficult to produce a perfectly symmetrical phenotype, particular if it is exaggerated in size and subject to intense directional selection (see next section). Asymmetries in different morphological characters of the same individuals are frequently not positively correlated (e. g. Parsons, 1990), since different characters do not necessarily belong to the same developmental unit and characters therefore do not develop simultaneously. Finally, I would like to stress that FA is but one measure of developmental stability. Others include the frequency of morphological and behavioural phenodeviants (Rasmuson, 1962; Markow & Gottesman, 1993), but also deviants in other dimensions such as physiology and immunology (Zakharov, 1992).

FA is not easy to measure because the magnitude is often minute (Palmer & Strobeck, 1986). Studies of FA must fulfill the following minimum requirements: (i) the character must demonstrate the characteristics of FA (a normal distribution of signed left-minus-right character values with a mean value of zero); and (ii) the measure of FA is repeatable between measurements by the same observer. These have only been fulfilled by a few studies (Møller, 1992a; 1993d; Møller & Eriksson, 1994a, b; Møller & Höglund, 1991).

In the following four sections I briefly review the importance of developmental stability for sexual selection by (i) describing the relationship between patterns of developmental stability and mode of selection; (ii) assessing the evidence for sexual selection in relation to developmental stability; (iii) describing the evidence for assessment of FA; and (iv) discussing the benefits accrueing to individuals that choose symmetrical partners.

Patterns of developmental stability and mode of selection

The patterns of developmental stability of traits are influenced by their recent history of selection. Characters that have been subject to a recent history of net directional selection demonstrate elevated levels of FA while morphological characters subject to a stabilizing selection regime have low levels of FA, with a mean asymmetry typically less than one per cent of the size of the character. Several experiments on *Drosophila* and *Mus* demonstrate that directional selection causes a deterioration of developmental homeostasis as measured in terms of FA (reviewed by Møller & Pomiankowski, 1993b). Similarly, the incorporation of new mutants into the genome is generally associated with increased morphological variability and FA (Clarke & McKenzie, 1987; reviewed by Møller & Pomiankowski, 1993a).

The phenotypic and genetic variance of a character is also influenced by the mode of selection. Stabilizing selection tends to result in a decreased phenotypic and genetic variance because stabilizing selection also selects for an increased number of genetic modifiers that mask the expression of extreme phenotypes as first suggested by Schmalhausen (1949). Directional selection results in selection against genetic modifiers which control development, and this gives rise to increased phenotypic and genetic variance provided the selection pressure does not completely deplete genetic variance.

The second general pattern is that larger characters demonstrate larger degrees of developmental instability because they are more costly in terms of energy and take longer time to produce. Therefore, there are higher probabilities of encountering stressful situations during development of a large as compared to a small character given the same genetic and environmental conditions.

The general patterns of morphological variance in relation to the prevailing mode of selection can readily be applied to sexual selection. Secondary sexual characters are characterized by their exaggeration compared to homologous characters in conspecific females and in males of many closely related species. This means that secondary sexual characters often have been subject to a recent history of net evolutionary change. A number of studies has demonstrated an elevated level of FA in secondary sexual characters as compared to other morphological traits, while other studies have been unable to demonstrate increased FA (table I). Many

TABLE I. Studies assessing the level of fluctuating asymmetry in secondary sexual characters and the relationship between fluctuating asymmetry and the size of secondary sexual characters compared with ordinary morphological characters.

[Estudios que establecen el nivel de fluctuación de asimetría en caracteres sexuales secundarios y la relación entre la fluctuación de la asimetría y el tamaño de los caracteres sexuales secundarios comparado con caracteres morfológicos ordinarios.]

Greater relative asymmetry	Relationship	Character	Species	References
Yes	Negative	tail	Barn swallow	Møller (1990, 1993a, 1993d,1994)
Yes	Negative	ocelli	Peacock	Manning & Hartley (1991)
Yes	Negative	cerci	Earwig	Radesäter & Halldórsdottir (1993)
Yes	Negative	spur	Pheasant	Sullivan et al. (1993)
Yes[1]	Negative	feathers	Birds	Møller & Höglund (1991)
Yes	Negative	spurs	Birds	Møller (1992a)
Yes	Negative	horns	Beetles	Møller (1992a)
Yes?	Negative	canines	Primates	Manning & Chamberlain (1993)
	Negative	feathers (preferred traits)	Birds	Møller (1993b)
No	Negative	petals	Plants	Møller & Eriksson (1993)
		feathers (single ornaments)	Birds	Møller & Pomiankowski (1993c)
No	Negative	petals	Fireweed	Møller (1994)
	None (negative?)	tail	Sunbird	Evans & Hatchwell (1993)
	None	feathers (non-preferred traits)	Birds	Møller (1993b)
	None	feathers (multiple ornaments)	Birds	Møller & Pomiankowski (1993c)
No	None	feathers	Birds	Balmford et al. (1993)
No	None	feathers	Whydahs	Barnard (MS)
?	Positive	antlers	Moose	Solberg & Solberg (1993)
?	Negative	antlers	White-tailed deer	Møller et al. (MS)

[1] Higher asymmetry in males of sexually dimorphic species than in males of monomorphic species.

of these mean levels of asymmetry are more than an order of magnitude larger than those of ordinary morphological characters, and this might make asymmetry easily perceived. The most likely explanation for the absence of increased developmental instability of secondary sexual characters is that they have been subject to a recent history of stabilizing selection. This appears to be the case for the tail ornaments of black grouse *Tetrao tetrix* (R. V. Alatalo, J. Höglund and A. Lundberg pers. comm.). Another potential reason is that sampling may not have been sufficiently extensive and unbiased. Floral traits did not demonstrate larger FA than leaf traits (Møller & Eriksson, 1994a), but this is probably due to the overall extensive phenotypic plasticity of plants compared with animals.

The relationship between FA and the size of secondary sexual characters is predicted to be U-shaped under a stabilizing selection regime (Møller & Pomiankowski, 1993b), but a number of studies have demonstarted clearly negative relationships which differ dramatically from the patterns for ordinary morphological characters (table I). This suggests that some individuals are able to develop symmetrical secondary sexual characters despite the size of these characters. Alternatively, this pattern may suggest that asymmetry is more costly for individuals with larger as compared to individuals with smaller sex traits (Evans, 1993). One

TABLE 2. Studies assessing sexual selection in relation to fluctuating asymmetry.
[Estudios que establecen la selección sexual en relación a la fluctuación de la asimetría.]

Evidence	Character	Species	References
mating	tail	Barn swallow[1]	Møller (1990, 1992b, 1993a, d, e)
mating	colour	Zebra finch[1]	Swaddle & Cuthill (1994)
mating	wing	Fruitflies	Markow & Ricker (1992)
mating, fighting	wing	Scorpionflies	Thornhill (1992a, b, c,), Thornhill & Sauer (1992)
mating	wing	Dungfly	Liggett et al. (1993)
mating	cerci	Earwig	Radesäter & Halldórsdottir (1993)
none	skeletal	Cricket frog	Ryan et al. (1993)
mating	skeletal	Human	Grammer & Thornhill (MS);Thornhill (MS)
mating	petals	Plants[1]	Møller (1994), Møller & Eriksson (1994b)
none	tail	Paradise whydah[1]	Oakes & Barnard (1994)
none	wing, stridulatory teeth	Decorated cricket	Eggert & Skaluk (MS)
mating	tibia	Field cricket	Simmons (MS)
mating	wing	Domestic fly	Møller (MS)
mating	son	Grasshopper	Møller (MS)
mating	skeletal	Pupfish	Kodric-Brown (MS)
none	colour	Guppy	Nordell (MS)
mating	skeletal	Crows	Saino (MS)
mating	chelae	Crabs	Kieser & Groeneveld (MS)

[1] Experimental manipulations of asymmetry.

experimental study of flight performance in relation to symmetry in ornaments clearly did not support this hypothesis (Møller, 1991). The absence of a negative relationship suggests that the trait currently is subject to a stabilizing mate preference (Møller, 1993b; Møller & Pomiankowski, 1993b). Other reasons are that sample sizes have sometimes been too small to accept the null hypothesis of no relationship (e. g. Evans & Hatchwell, 1993), or that species without any evidence of sexula selection and with widely differing ecologies are lumped into a single analysis (Balmford et al., 1993). Furthermore, delection of museum specimens with moult in non-ornamental feathers from samples (as in the study by Balmford et al., 1993) may cause serious bias if highly asymmetric individual moult more slowly than others.

In conclusion, a number of studies have demonstrated elevated levels of FA in secondary sexual characters and some of these traits demonstrate a negative relationship between asymmetry and character size, which differs dramatically from the pattern in other morphological characters.

Sexual selection and fluctuating asymmetry

Does FA matter in sexual selection? A number of observational and quasi-experimental studies has demonstrated that males with elevated levels of asymmetry in secondary sexual characters more often loose fights over mates (table II). Other studies have shown that females prefer males with low levels of asymmetry in secondary sexual characters (table II). Finally, some studies of FA in characters supposedly not involved in sexual selection have still demonstrated a disadvantage during mating (table II). This is likely to be due to assessment of overall behaviour as influenced by asymmetry rather than actual assessment of FA. Alternatively, FA may simply reflect an overall poor phenotype. Some studies have been unable to demonstrate a sexual selection advantage with respect to FA (table II), and this may be due to a number of different reasons. First, arbitrarily chosen morphological characters may not be important in the context of sexual selection. Second, asymmetry in the character in question cannot be readily assessed if both sides are not displayed simultaneously. Third, negative results may be due to experimental designs which do not allow determination of whether females prefer large ornaments, symmetrical ornaments, or both (Oakes & Barnard, 1994).

In conclusion, there is some evidence that asymmetry in secondary sexual characters, but also in ordinary morphological characters is important in sexual selection.

Assessment of fluctuating asymmetry

An obvious question arising from the apparent advantage accrueing to individuals with symmetrical secondary sexual character is whether the levels of FA can be assessed. A number of studies has demonstrated that birds are able to handle asymmetry as a category and use it in discrimination learning (Rensch, 1958; Delius & Habers, 1978; Delius & Nowak, 1982). Field and laboratory experimental manipulations of the level of asymmetry have also shown that females and pollinators discriminate against asymmetry (Møller, 1992b; 1993c; 1994; Swaddle & Cuthill, 1994). One study claims to have shown a female preference for males with more asymmetrical ornaments (Oakes & Barnard, 1994), but the experimental design did not allow assessment of whether ornament size or ornament symmetry was the target of selection.

The assessment of FA by animals may potentially have a number of different origins. First, the sensory system may have pre-existing biases for symmetry because almost the entire animate world displays some kind of symmetry. All enemies, parasites, food items, competitors, and potential mates display symmetry at one level or another (Møller, 1992c). This fact may dramatically have affected the evolution of sensory systems to be able to discriminate between symmetry and asymmetry. Second, individuals may learn to prefer symmetry if it for example is associated with the acquisition of food. This may be the case for predators searching for cryptic prey on a tree trunk or pollinators receiving higher pollinator rewards at symmetric flowers (Møller, 1994; Møller & Eriksson, 1994b). Third, females may discriminate against males with asymmetrical secondary sexual characters because of a mate preference for symmetrical males that has evolved within an ornamented clade.

In conclusion, the ability to assess asymmetry may be due to a pre-existing sensory bias, learning, or a genetically based mate preference.

Fitness benefits from mating with symmetrical males

Females may obtain three different kinds of fitness benefits from mating with symmetrical males; viz. (i) direct benefits, (ii) attractive sons, and (iii) viable offspring. The optimal phenotype is symmetrical and even slight deviations from symmetry may severely affect performance of motile organisms (Møller, 1991; Thomas, 1993). Females may obtain direct benefits from their choice of symmetrical males if males provide direct benefits such as territories, nuptial gifts and paternal care. This may be the case in scorpionflies which provide females with nuptial gifts (Thornhill, 1992a). Barn swallow males *Hirundo rustica* with experimentally altered asymmetry in their tail ornaments provide relatively and absolutely more parental care if their tails were highly asymmetric (Møller, 1993c). This suggests that asymmetrical, unattractive males provide more, not less, parental care than symmetrical, attractive males. The second benefit of production of attractive, symmetrical sons has not been investigated empirically, although the mechanism is likely because of female preferences for males with symmetrical secondary sexual characters. The third benefit is production of viable offspring. Symmetrical morphological characters are reliable predictors of survival prospects and parasite infestation of males (Møller, 1992d, 1993a; Thornhill, 1992a; Polack, 1993). Females mating with symmetrical males will gain an indirect advantage if there is a genetic basis for viability. Alternatively, females may experience a good genes advantage because developmental stability has a genetic component (review in Møller & Thornhill MS). Females mating with symmetrical males will therefore produce genetically superior sons that are symmetrical.

In conclusion, there is some evidence for both direct and indirect fitness benefits of choice of symmetrical mating partners.

Conclusion

A considerable amount of data have been collected to test the hypothesis that developmental stability plays a role in sexual selection. The evidence in support of the hypothesis is substantial although evidence that appears to refute it is also present. Most studies have investigated the importance of fluctuating asymmetry in secondary sexual characters assessed by the visual sensory system. However, similar principles could equally well apply to secondary sex traits assessed by other sensory systems.

Summary

The role of developmental stability of secondary sexual characters for sexual selection theory is reviewed. Developmental stability of otherwise bilaterally or radially symmetrical characters is measured as the degree of fluctuating asymmetry, the frequency of morphological or behavioural phenodeviants, or the frequency of deviants in other dimensions. The relationship between developmental stability and the prevailing mode of selection during recent evolutionary history is decreased stability under directional selection and increased stability under stabilizing selection. Sexual selection is characterized by a recent evolutionary history of continuous directional selection, and this selects for reduced developmental stability. Large secondary sexual characters demonstrate the smallest degrees of fluctuating asymmetry in some but not in other species, and this differs from the patterns of asymmetry in ordinary morphological characters. A number of studies has found that symmetrical individuals more often win at fights over mates or are chosen as mates by individuals of the choosy sex. A number of other studies has demonstrated that small, imperceivable asymmetries in ordinary morphological characters are associated with reduced mating success. Field and laboratory experiments have shown that individuals of the choosy sex are able to discriminate between potential mates on the basis of asymmetry. Females may obtain direct benefits from choosing a mate with symmetrical secondary sexual characters because high developmental stability may be associated with intensive male parental care. Alternatively, females may obtain indirect benefit because sons will inherit the attractiveness of the symmetrical traits of their fathers, or because developmental stability signals high heritable viability and fluctuating asymmetry is selected against during episodes of natural selection.

Resumen

Estabilidad del desarrollo, selección sexual, y evolución de los caracteres sexuales secundarios.

Se revisa el papel de la estabilidad del desarrollo de los caracteres sexuales secundarios, para la teoría de la selección sexual. La estabilidad del desarrollo de caracteres bilateral o radialmente simétricos se mide como el grado de fluctuación de asimetría, la frecuencia de desviaciones fenotípicas morfológicas o comportamentales, o la frecuencia de desviaciones en otras dimensiones. La relación entre la estabilidad del desarrollo y el modo predominante de selección durante la historia evolutiva reciente, es de disminución de la estabilidad bajo selección direccional y de aumento bajo selección estabilizante. La selección sexual se caracteriza por una historia evolutiva reciente de selección direccional contínua, y ésta tiende a la estabilidad de desarrollo reducida. Los caracteres sexuales secundarios grandes demuestran los grados mas pequeños de fluctuación de la asimetría en algunas especies pero no en otras, y ésta difiere de las pautas de asimetría en caracteres morfológicos ordinarios. Algunos estudios han encontrado que los individuos simétricos ganan mas a menudo en las luchas para conseguir pareja o son mas elegidos como tal por individuos del sexo que elige. Otros estudios han demostrado que asimetrías pequeñas e imperceptibles en caracteres morfológicos ordinarios, están asociados con éxitos de apareamientos reducidos. Experimentos de campo y laboratorio han demostrado que los individuos del sexo que elige son capaces de discriminar entre parejas potenciales sobre la base de la asimetría. Las hembras pueden obtener beneficios directos por elegir una pareja con caracteres sexuales secundarios simétricos, debido a que la alta estabilidad de desarrollo puede estar asociada con un gran cuidado parental por parte del macho. Alternativamente, las hembras pueden obtener beneficios indirectos debido a que los hijos heredarán el atractivo de los rasgos simétricos de sus

padres, o debido a que la estabilidad del desarrollo de las señales alcanza una viabilidad heredable y la fluctuación de la asimetría es seleccionada en contra por la selección natural.

Acknowledgments

I am grateful for the generous invitation by the Organizing Committee of the XXIII International Ethological Conference to present my ideas on developmental stability and sexual selection. R.V. Alatalo, P. Barnard, J. Höglund, J. Kieser, A. Kodric-Brown, A. Lundberg, S. Nordell, N. Saino, L. W. Simmons and R. Thornhill kindly provided unpublished information. My research was supported by grants from the Swedish Natural Science Research Council.

References

Balmford, A., Jones, I.L. & Thomas, A.L.R., 1993. On avian asymmetry: Evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B*, 252:245-251.

Clarke, G.M. & McKenzie, J.A., 1987. Developmental stability of insecticide resistant phenotypes in blowfly: A result of canalizing natural selection. *Nature*, 325:345-346.

Darwin, C., 1871. *The descent of man, and selection in relation to sex.* London: John Murray.

Delius, J.D. & Habers, G., 1978. Symmetry: Can pigeons conceptualize it? *Behav. Biol.*, 22:336-342.

Delius, J.D. & Nowak, B., 1982. Visual symmetry recognition by pigeons. *Psychol. Res.*, 44:199-212.

Eggert, A.K. & Sakaluk, S., 1994. Fluctuating asymmetry and variation in the size of courtship food gifts in decorated crickets. *Am. Nat.*, (in press)

Evans, M.R., 1993. Fluctuating asymmetry as a tax of ornamentation. *Proc. R. Soc. Lond. B*, (in press).

Evans, M.R. & Hatchwell, B.J., 1993. New slants on ornament asymmetry. *Proc. R. Soc. Lond. B*, 251:171-177.

Liggett, A.C., Harvey, I.F. & Manning, J.T., 1993. Fluctuating asymmetry in *Scatophagus stercoraria*: Successful males are more symmetric. *Anim. Behav.*, 45:1045-1048.

Ludwig, W., 1932. *Das Rechts-Links Problem im Tierreich und beim Menschen.* Berlin: Springer.

Manning, J.T. & Hartley, M.A., 1991. Symmetry and ornamentation are correlated in the peacock's train. *Anim. Behav.*, 42:1020-1021.

Manning, J.T. & Chamberlain, A.T., 1993. Fluctuating asymmetry, sexual selection and canine teeth in primates. *Proc. R. Soc. Lond. B*, 251:83-87.

Markow, T.A. & Gottesman, I.I., 1993. Behavioral phenodeviance: A lerneresque conjecture. *Genetica*, (in press).

Markow, T. & Ricker, J.P., 1992. Male size, developmental stability, and mating success in natural populations of three *Drosophila* species. *Heredity*, 69:122-127.

Møller, A.P., 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.*, 40:1185-1187.

Møller, A.P., 1991. Sexual ornaments size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond. B*, 243:59-62.

Møller, A.P., 1992a. Patterns of fluctuating asymmetry in weapons: Evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. B* 248:199-206.

Møller, A.P., 1992b. Females prefer large and symmetrical ornaments. *Nature*, 357:238-240.

Møller, A.P., 1992c. Fluctuating asymmetry and the evolution of signals. In: *Workshop on Behavioural Mechanisms in Evolutionary*

Perspective: 96-98. (P. Bateson & M. Gomendio, Eds.). Madrid: Instituto Juan March de Estudios e Investigaciones.

Møller, A.P., 1992d. Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characters. *J. Evol. Biol.*, 5:691-699.

Møller, A.P., 1993a. Sexual selection in the barn swallow (*Hirundo rustica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. *Evolution*, (in press).

Møller, A.P., 1993b. Patterns of fluctuating asymmetry in sexual ornaments predict female choice. *J. evol. Biol.*, (in press).

Møller, A.P., 1993c. Symmetrical male sexual ornaments, paternal care and offspring quality. *Behav. Ecol.*, (in press).

Møller, A.P., 1993d. Morphology and sexual selection in the barn swallow (*Hirundo rustica*) in Chernobyl, Ukraine. *Proc. R. Soc. Lond. B*, 252:51-57.

Møller, A.P., 1993e. Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.*, 32:371-376.

Møller, A.P., 1994. The function of symmetric flowers. *J. evol. Biol.*, (in press).

Møller, A.P. & Eriksson, M., 1993a. Patterns of fluctuating asymmetry in flowers: Implications for sexual selection in plants. *J. evol. Biol.*, 7:97-113.

Møller, A.P. & Eriksson, M., 1994b. Flower asymmetry and sexual selection in plants. *Ecology*, (in press).

Møller, A.P. & Höglund, J., 1991. Patterns of fluctuating asymmetry in avian feather ornaments: Implications for models of sexual selection. *Proc. R. Soc. Lond. B*, 245:1-5.

Møller, A.P. & Pomiankowski, A., 1993a. Fluctuating asymmetry and sexual selection. *Genetica*, 89:267-279.

Møller, A.P. & Pomiankowski, A., 1993b. Punctuated equilibria or gradual evolution: The importance of fluctuating asymmetry. *J. theor. Biol.*, 161:359-367.

Møller, A.P. & Pomiankowski, A., 1993c. Why have animals got multiple sexual ornaments? *Behav. Ecol. Sociobiol.*, 32:167-176.

Oakes, E.J. & Barnard, P., 1993. Fluctuating asymmetry and mate choice in paradise whydahs (*Vidua paradiaea*): An experimental manipulation. *Anim. Behav.*, (in press).

Palmer, A.R. & Strobeck, C., 1986. Fluctuating asymmetry: Measurement, analysis, patterns. *A. Rev. Ecol. Syst.*, 17:391-421.

Parsons, P.A., 1990. Fluctuating asymmetry: An epigenetic measure of stress. *Biol. Rev.*, 65:131-145.

Polack, M., 1993. Parasitic infection increases fluctuating asymmetry of male *Drosophila nigrospiracula*: Implications for sexual selection. *Genetica*, (in press).

Radesäter, T. & Halldórsdottir, H., 1993. Fluctuating asymmetry and forceps size in earwigs, *Forficula auricularia*. *Anim. Behav.*, 45:626-628.

Rasmuson, M., 1960. Frequency of morphlogical deviations as a criterion of developmental stability. *Hereditas*, 46:511-536.

Rensch, B., 1958. Die Wirksamkeit ästhetischer Faktoren bei Wirbeltieren. *Z. Tierpsychol.*, 15:447-461.

Ridley, M., 1992. Swallows and scorpionflies find symmetry is beautiful. *Science*, 257:327-328.

Ryan, M.J., Warkentin, K M., McLelland, B.E. & Wilczynski, W., 1993. Fluctuating asymmetries and advertisement call variation in the cricket frog, *Acris crepitans*. *Anim. Behav.*, (in press).

Schmalhausen, I.I., 1949. *Factors of evolution*. Philadelphia and Toronto: Blakiston.

Solberg, E.J. & Saether, B.-E., 1993. Fluctuaying asymmetry in the antlers of moose (*Alces alces*): Does it signal male quality? *Proc. R. Soc. Lond. B.*, 254:251-255

Sullivan, M.S., Robertson, P. A. & Aebischer, N. A., 1993. Fluctuating asymmetry measurement. *Nature*, 361:409-410.

Swaddle, J.P. & Cuthill, I.C., 1994. Preference for symmetry males by female zebra finches. *Nature*, 361:165-166.

Thomas, A.L.R., 1993. On the aerodynamics of bird tails. *Phil. Trans. R. Soc. Lond. B*, (in press).

Thornhill, R., 1992a. Fluctuating asymmetry and the mating system of the Japanese scorpionfly, *Panorpa japonica*. *Anim. Behav.*, 44:867-879.

Thornhill, R., 1992b. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*, Mecoptera). *Behav. Ecol.*, 3:277-283.

Thornhill, R., 1992c. Fluctuating asymmetry, interspecific aggression and male mating tactics in two species of Japanese scorpionflies. *Behav. Ecol. Sociobiol.*, 30:357-363.

Thornhill, R. & Sauer, P., 1992. Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. *Anim. Behav.*, 43:255-264.

Zakharov, V.M., 1992. Population phenogenetics: Analysis of developmental stability in natural populations. *Acta Zool. Fenn.*, 191:7-30.

(Recibido: diciembre 1993)