In more detail, 13 (57%) of 23 colonies sampled were judged to have a singly mated queen (allozyme analysis showed that worker–female relatedness equalled 0.72). The other 10 colonies (43%) had a doubly or triply mated queen (worker–female relatedness was 0.43). It is a fair assumption that workers can detect multiple mating in their queen but not assess her exact mating frequency. This allows the colonies with double and triple mating to be treated as one class[11]. The RA of the singly mating class was therefore 0.72/0.25 = 2.9 (worker–male relatedness equals 0.25 independently of mating frequency). Similarly, the RA of the multiply-mating class was 0.43/0.25 = 1.7. The average per colony sexual productivity of the two classes was equal. Consequently, following a method of Boomsma and Grafen[6], the expected sex ratio (as the proportion of investment in females) of (1) the singly mating class is 1.0 (all females), (2) the multiply mating class is 0.14 (male-biased), and (3) the population is 0.63 (the RA of the multiply mated class expressed as a fraction). These predictions follow directly from the theory outlined above. Specifically, the multiply mating class is relatively large enough to 'balance' the all-female production of the singly mating one, producing a male-biased class-specific sex ratio that decreases the population sex ratio until equilibrium is reached at a level equalling the RA of the multiply mating class[6].

The observed population ratio (0.67) and the predicted level (0.63) were satisfyingly close. Also, as already stated, sex ratios were split in the directions predicted. However, the singly mating class clearly did not produce females exclusively (Fig. 1). There are several possible explanations for this, one being that workers may make occasional mistakes in judging colony RA and so rear an inappropriate sex ratio[10]. The mating frequency in a few colonies may also have been misclassified by the observer, since some queens probably mated with two males bearing the same marker allele[11].

Conclusion

Sundström's results provide the best evidence yet of split sex ratios arising from workers' responses to their variable RA. Moreover, they also support worker-controlled sex allocation[1], the idea that within-population sex ratio variation may often stem from variable RA[5,6] and Fisherian theory in general[1,2,12]. It would now be interesting to check similar systems, in other species, for split sex ratios. In addition, testing for worker assessment of RA using methods which are independent of the examination of sex allocation is also desirable. Split sex-ratio theory has clearly given new impetus to the study of sex ratios and social evolution in insects.

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References

1 Trivers, R.L. and Hare, H. (1976) *Science* 191, 249–263

2 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon

3 Hamilton, W.D. (1964) *J. Theor. Biol.* 7, 1–52

4 Alexander, R.D. and Sherman, P.W. (1977) *Science* 196, 494–500

5 Boomsma, J.J. and Grafen, A. (1990) *Evolution* 44, 1026–1034

6 Boomsma, J.J. and Grafen, A. (1991) *J. Evol. Biol.* 3, 383–407

7 Grafen, A. (1986) *J. Theor. Biol.* 122, 95–121

8 Boomsma, J.J. (1991) *Trends Ecol. Evol.* 6, 92–95

9 Boomsma, J.J. (1993) in *Queen Number and Sociality in Insects* (Keller, L., ed.), pp. 86–109, Oxford University Press

10 Ratnieks, F.L.W. (1991) *Evolution* 45, 281–292

11 Sundström, L. (1994) *Nature* 367, 266–268

12 Benford, F.A. (1978) *J. Theor. Biol.* 72, 701–727

13 Nonacs, P. (1986) *Q. Rev. Biol.* 61, 1–21

14 Herbers, J.M. (1990) *Am. Nat.* 136, 178–208

15 Pamilo, P. (1990) *Behav. Ecol. Sociobiol.* 27, 31–36

16 Crozier, R.H. and Pamilo, P. (1993) in *Evolution and Diversity of Sex Ratio in Insects and Mites* (Wrensch, D.L. and Ebbert, M.A., eds), pp. 369–383, Chapman & Hall

17 Frank, S.A. (1987) *Behav. Ecol. Sociobiol.* 20, 195–201

18 Mueller, U.G. (1991) *Science* 254, 442–444

19 Queller, D.C., Strassmann, J.E., Solís, C.R., Hughes, C.R. and DeLoach, D.M. (1993) *Nature* 365, 639–641

The science of symmetry in biology

Symmetry has long been an important concept in mathematics and physics[1,2], but in biology its study was largely limited to morphology and systematics until 1953 when Mather revealed the value of studying variation in the degree of bilateral symmetry within a population[3]. The difference in sternopleural bristle number between the left and the right side of fruit flies, *Drosophila melanogaster*, was shown to be larger in some inbred lines of flies than in outbred ones. Direction of asymmetry (for example, left > right) was not heritable, but the magnitude of asymmetry was such that it could be increased through direct selection under laboratory conditions. More strikingly, it was discovered that selection for high or low bristle number increased the associated asymmetry[4].

Three kinds of bilateral asymmetry have been described, based on the form of the distribution of differences between right and left values. Asymmetry that shows a normal distribution around a mean of zero is called fluctuating asymmetry (FA), in contrast to directional asymmetry, in which the mean is biased to the left or right (e.g. handedness in humans). Antisymmetry, in turn, refers to distributions in which symmetrical individuals are relatively uncommon (or absent) but the asymmetries in a population show no directional bias (e.g. giant claws of male fiddler crabs, *Uca lactea*). Assuming that each member of a bilateral trait showing FA is the product of the same genes, departure from the *a priori* optimal state, perfect bilateral symmetry (see below), is viewed as a reflection of disrupted development, that is, developmental instability. The assumption of genetic commonality (identical genes striving for an identical purpose) is limited to FA. It is not a feature of other indices of developmental instability (e.g. morphological variance[5] and antisymmetry[6]), which all lack an optimal state as a reference point.

In June last year, more than 50 scientists gathered in Tempe, AZ, USA, to survey what we have learned about asymmetry and related variables*. FA is now known to be diagnostic for a wide range of environmental and genetic stressors borne during development. In humans, FA is associated with Down's syndrome and other chromosomal anomalies, inbreeding, maternal disease, maternal alcohol consumption and parental tobacco intake[7–9]. Moreover, particular asymmetries (e.g. in dermal ridge patterns) may be associated with particular disorders (e.g. schizophrenia) but not with others (e.g. manic depressive illness)[10]. Thus, asymmetry in traits whose ontogenies are

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well-characterized may allow a means of distinguishing periods of heightened sensitivity ('windows of vulnerability') to certain stressors associated with phenodeviance later in life (Robert Vrijenhoek, Center for Theoretical and Applied Genetics, Rutgers University, New Brunswick, NJ, USA). In pigtailed macaques (*Macaca nenestrina*), for example, stressing the mother by repeated capture, between 30 and 130 days of pregnancy leads to increased dermatoglyphic FA in her progeny[11].

Fluctuating asymmetry and phenotypic quality

The most important advance in our understanding of fluctuating asymmetry is the discovery that FA is a good measure of phenotypic quality. Indeed, it may be the best measure we have. But differences in FA between individuals are often small and easily overwhelmed by measurement error. Thus, statistical techniques have been developed for assessing measurement error and removing it from measures of FA (Richard Palmer, University of Alberta, Edmonton, Canada). Phenotypic quality is a key evolutionary variable, defined as the expected ability of an individual to succeed in life, that is, to express high inclusive fitness.

For bilaterally symmetrical traits showing FA, we are permitted to assume that the organism is trying to be symmetrical (for optimization reasons mentioned below). Therefore, inability to achieve symmetry is a measure of inability to achieve a desired state. For other measures of quality, by contrast, we usually only know an optimal range (e.g. large size) and not an optimal value (symmetry itself). If symmetry provides a handy way of ranking individuals according to phenotypic quality (and therefore often genotypic quality), then organisms are expected to use symmetry as a cue in mate choice, and sexual selection may favour the evolution of display traits in males that easily reveal asymmetry. In fact, in swallows, and ourselves, individuals respond directly to symmetry and prefer the most symmetrical members of the opposite sex (for a detailed treatment of these points with supporting references see Watson and Thornhill's recent *TREE* review[12]). Sexually-selected traits, whether they be exaggerated bird plumage used in courtship, or spurs used in combat, typically show between five and ten times as much FA as comparable non-sexually selected traits (Anders Møller, Uppsala University, Sweden). In some species, individuals with the largest secondary sexual structures also have the most symmetrical ones, while in others, average-sized structures are the most symmetrical. This confirms the value of FAs in characterizing the adaptive topography of other traits.

Genetics of symmetry

Parasites are a key factor affecting sexual selection in many species, so it is noteworthy that there are strong, positive associations between parasite load and asymmetry in insects, birds and humans, both because parasites can cause asymmetry[13] and because asymmetrical individuals are more likely to become infected[14]. Heterozygosity may provide some protection from parasites, especially, for example, at major histocompatibility (MHC) loci, but also more generally. Since heterozygosity is heritable[15], pressure from parasites may give added importance to symmetry in mate choice to the degree that heterozygosity is positively associated with symmetry.

Within populations of rainbow trout (*Oncorhyncus mykiss*) and cutthroat trout (*Oncorhyncus clarki*), there exist significant negative correlations between individual heterozygosity (measured across > 10 loci) and FA[16,17]. In rainbow trout, individuals heterozygous at just two of these loci are more symmetrical than the respective homozygotes[16]. But in rainbow trout, individuals who carry one null and one active allele at a lactate dehydrogenase locus (LDH-B1) locus express higher FA than active allele homozygotes, even though they are heterozygous (Robb Leary, University of Montana, Missoula, MT, USA). Beyond these, data are sparse and show no association (e.g. house mice, *Mus musculus*[18]). Comparisons of populations within a species show negative associations between heterozygosity and mean FA (e.g. lizards, *Uta stansburiana*) as well as no association (e.g. pocket gophers, *Thomomys bottae*) (Geoffrey Clarke, CSIRO Division of Entomology, Canberra, Australia). Inbred species, such as cheetahs (*Acinonyx jubatus*), may show elevated FAs compared to outbred ones, such as leopards, *Panthera pardus*, but even this has been questioned and is not a general trend.

A comparison between hybrids and parental populations may help to explain some of these differences. Two different forces are imagined to effect FA in hybrids. Hybrids are likely to show greater heterozygosity than parental stocks because of divergent selection in the two stocks. But this same selection will have produced divergent genotypes which, when combined, may be less co-adapted than parental stocks. This will be especially true of recent hybrids which have had little time to re-evolve co-adaptation. In turn, long-standing hybrids between subspecies of bluegill sunfish (*Lepomis macrochirus*) show the same degree of FA as the parental stocks[19], whereas recent hybrids of two species of sunfishes (*Enneacanthus* spp.) show elevated FAs[20]. In crosses between *Drosophila melanogaster* and *D. simulans*, this elevation in FA occurs only in females[21]. It is absent in males, even though there is no history of hybridization.

A breakdown of genic co-adaptation can also occur when otherwise rare alleles are fixed into a gene pool via drift in small insular populations or by strong directional selection. A dramatic example of the latter is provided by the Australian blowfly (*Lucilia cuprina*) in which an otherwise rare allele that disrupted development spread during the 1960s because it conferred resistance to a pesticide which was then in use. At first, FA increased but it then decreased steadily to its original value, presumably because modifier genes were selected which integrated the new allele into the genome[6]. Selection for new or rare alleles conferring resistance against parasites may disrupt host development in a similar manner. But contrary to the blowfly example, FA among resistant hosts could remain high across generations because novel resistance-conferring alleles continually cycle between high and low frequency via frequency-dependent interactions between host and parasite genomes. This raises the intriguing possibility, that high FA may, under some conditions, reveal resistance against disease. It is interesting that whisker FA in lions is negatively correlated with longevity in males, but positively correlated in females[22]. The reasons for this are unknown.

Symmetrical transformations

Mathematicians define symmetry as any transformation of one set of data rendering it identical, or isomorphic, to a second set[1]. The two sets are then said to be symmetrical with reference to the transformation. Bilateral symmetry involves a mirror-image transformation, whereas radial symmetry involves rotating a set of data a fixed number of degrees around a central point. Different kinds of radial symmetry may be generated by differences in the number of symmetrical transformations possible in 360° (e.g. four rotations of 90° or six of 60°). Analogs to FA can be constructed (Karl Freeman, Wayne State University, Detroit, MI, USA), and Møller (unpublished) has demonstrated that flowers altered to become radially asymmetrical attract fewer pollinators. Mathematicians have shown that in the calculus of variations, the solution to optimization problems will often possess symmetries. For example, the most symmetrical three-dimensional object (the sphere) maximizes volume per unit surface area. Likewise, a locomotor apparatus, such as wings, must usually be selected for symmetry in order to minimize costs associated with asymmetry, such as energy expenditure in flight. This suggests, of course, that some species will be more strongly selected for particular symmetries than will others (e.g. wing symmetry in migratory versus nonmigratory birds).

Symmetry and social relations

It seems likely that evaluating the phenotypic quality (and, therefore, FA) of others is useful in a variety of contexts beyond mate choice; for example, in allocating resources to offspring and other kin[23]. Likewise, organisms are expected to value phenotypic quality in their reciprocal partners. This may help explain why we attend to physical attractiveness so early in life (e.g. at six months of age[24]) and continually thereafter.

Symmetry between individuals may be important in social relations. By definition, reciprocal altruism requires a degree of symmetry (regular reversal of donor–recipient roles). In species of seabass (Serranidae), more-symmetrical egg trading is associated with greater economy of design (reduction in testes size) (Ref. 25). Likewise, in baboons, *Papio* spp., the degree of symmetry in greetings exchanged between a pair of males is positively associated with the degree of cooperation between them[26]. Fair compromises of competing interests (such as between mates, or parents and offspring) will themselves be symmetrical and may reduce the costs of conflict. The deeper study of symmetry in biology promises many more exciting discoveries.

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References

1 Weyl, H. (1952) *Symmetry*, Princeton University Press
2 Lee, T.D. (1988) *Symmetries, Asymmetries and the World of Particles*, University of Washington Press
3 Mather, K. (1953) *Heredity* 7, 297–336
4 Thoday, J.M. (1958) *Heredity* 12, 401–415
5 Mitton, J.B. (1978) *Nature* 273, 661–662
6 McKenzie, J.A. and O'Farrell, K. *Genetica* (in press)
7 Markow, T.A. and Martin, J.F. (1993) *Ann. Hum. Biol.* 20, 389–394
8 Livshits, G. and Kobylianski, E. (1991) *Hum. Biol.* 63, 441–466
9 Kieser, J.A. (1992) *Ann. Hum. Biol.* 19, 513–520
10 Markow, T.A. (1992) *Psychol. Med.* 22, 295–305
11 Newell-Morris, L.L., Fahrenbruch, C.E. and Sackett, G.P. (1989) *Biol. Neonate* 56, 61–75
12 Watson, P.J. and Thornhill, R. (1994) *Trends Ecol. Evol.* 9, 21–25
13 Møller, A.P. (1992) *J. Evol. Biol.* 5, 691–699
14 Schall, J.J. and Calos, J.B. *Evolution* (in press)
15 Mitton, J.B., Schuster, W.S.F., Cothran, E.G. and De Fries, J.C. (1993) *Heredity* 71, 59–63
16 Leary, R.F., Allendorf, F.W. and Knudsen, K.L. (1983) *Nature* 301, 71–72
17 Leary, R.F., Allendorf, F.W. and Knudsen, K.L. (1984) *Am. Nat.* 124, 540–551
18 Wooten, M.C. and Smith, M.H. (1986) *J. Mamm.* 67, 725–732
19 Felley, J. (1980) *Copeia*, 18–29
20 Graham, J.H. and Felley, J.D. (1985) *Evolution* 39, 104–114
21 Markow, T.A. and Ricker, J.P. (1991) *Genetica* 84, 115–121
22 Packer, C. and Pusey, A.E. (1993) *Nature* 362, 595
23 Thornhill, R. and Gangestad, S.W. (1993) *Human Nature* 4, 237–269
24 Langlois, J.H., Ritter, J., Roggman, L.A. and Vaughn, L.S. (1991) *Dev. Psychol.* 27, 79–84
25 Fischer, E.A. and Petersen, C.W. (1987) *BioScience* 37, 482–489
26 Smuts, B.B. and Watanabe, J.M. (1990) *Int. J. Primatol.* 11, 147–172

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