

Why then do Lehmann and his colleagues not see any difference in the response of their primary and SV40-transformed cells to ionizing radiation? One possibility is that the p53 pathway is not functioning correctly in their primary cells. Several studies now indicate a very strong selection against p53 function during the establishment of cells in culture (for example, ref. 4) and it is possible to overcome the response to p53 through the activity of other genes^{5,6}. The difference in genetic stability between established cells and primary cells is, for example, well documented by the high frequency of gene amplification events found only in cell lines (for example, ref. 7). Alternatively, the problem may be methodological — as Kuerbitz *et al.* discuss, G2 checkpoint controls still

operate in their p53-deficient cells and care is needed to distinguish this from the G1 arrest¹. Not all policeman are equal, and some are more easily evaded than others!

D. P. Lane
*CRC Laboratories,
 Department of Biochemistry,
 Medical Sciences Institute,
 University of Dundee,
 Dundee DD1 4HN, UK*

1. Kuerbitz, S. J. *et al. Proc. natn. Acad. Sci. U.S.A.* **89**, 7491–7495 (1992).
2. Kastan, M. B. *et al. Cancer Res.* **51**, 6304–6311 (1991).
3. Hall, P. *et al. Oncogene* (in the press).
4. Harvey, P. M. & Levine, A. J. *Genes Dev.* **5**, 2375–2385 (1991).
5. Momand, J. *et al. Cell* **69**, 1237–1245 (1992).
6. Lu, X. *et al. Cell* **70**, 153–161 (1992).
7. Tlsty T. D. *et al. Science* **25**, 1425–1427 (1992).

Swallowing ornamental asymmetry

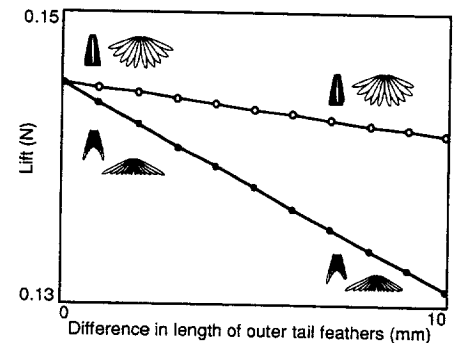
SIR — Møller¹ provides convincing evidence that the reproductive success of male swallows (*Hirundo rustica*) is independently increased by both the length and degree of symmetry of their outermost tail feathers. He suggests that the greater success of males with symmetrical tails arises not through an enhanced ability of males to provision their young or win intrasexual contests over females, but through female preferences for symmetrical as well as large ornaments. Because fluctuating asymmetry reflects an individual's inability to cope with environmental stress during trait development², Møller argues that preferences for symmetrical ornaments may have evolved because they enable females to choose high quality mates and so obtain "good genes" for their offspring¹.

Alternative explanations for the evolution and maintenance of tail symmetry are suggested by our work on the aerodynamics of bird tails³ showing that the lift generated by a tail depends on its angle of attack and the square of maximum continuous tail width. The aerodynamically optimum tail should therefore be triangular when spread and thus forked at rest. One drawback of a forked tail (like a swallow's) is that a high proportion of the lift that it produces is generated by its outermost feathers, and so any asymmetry in those feathers will greatly reduce lift (see figure). Furthermore, asymmetry will affect the distribution of lift across the tail and introduce large rolling and yawing forces which a bird could overcome only by flying with its tail at an angle. Therefore even a moderate degree of tail asymmetry will exert a profound effect on the manoeuvrability of male swallows (as Møller has already demonstrated experimentally⁴).

This has two important implications.

First, it suggests that symmetrical outer tail feathers may have evolved and been maintained primarily under natural rather than sexual selection. One reason for this is that the substantial reduction in agility associated with increased asymmetry is likely to have a considerable impact on the feeding efficiency of an aerial insectivore such as a swallow. Møller sought to refute this possibility by showing that manipulation of male tail symmetry does not affect the size attained by nestlings fed by males¹. But because tail elongation also has no effect on nestling size¹, but is known to reduce male foraging efficiency⁵, the size of nestlings is clearly not a reliable index of male feeding ability. If, instead, asymmetry does depress feeding efficiency substantially, it may well have a greater effect on male fitness than the 15–25% reduction in annual reproductive success attributed to female discrimination against males with artificially asymmetrical tails¹.

Second, the observed effects of tail symmetry on the mating success of male swallows need not necessarily arise through female preferences for symmetrical tails. For instance, the reduction in manoeuvrability caused by asymmetry may have substantial direct and indirect consequences for an individual's ability to compete intrasexually for mates. Again, evidence presented against this suggestion is unconvincing. Different symmetry treatments do not affect the average level of male–male aggression seen during three one-hour watches¹, but if such encounters are infrequent, the high sampling error associated with short watches may obscure real differences in aggression rates (mean values and ranges are not given). Moreover, no data are presented on the crucial issue of whether asymmetry treatments affect the



Effect of asymmetrical outer tail feathers on lift, calculated using a lifting surface model of tail aerodynamics³. Filled circles, a tail that is forked when at rest and triangular when spread; open circles, weaker effect of asymmetry on the lift of a tail that is triangular at rest. Both tails have an apex spreading angle of 120°, and an angle of incidence to the local flow direction of 10°; outer rectrices are 100 mm long. The variation in asymmetry considered (relative to outer rectrix length) corresponds to the range in mean relative asymmetry seen across males of 15 species with ornamental tails⁶, and is far less than the maximum degree of asymmetry produced by Møller's manipulations. The maximum asymmetry of 10 mm introduces a 13% reduction in total lift generated by the forked tail. This relative loss would diminish if the same absolute asymmetry occurred in a longer forked tail (in which the outermost rectrices contribute relatively less to the maximum continuous span of the spread tail). This may explain the greater effect of asymmetry on the mating success of males with shortened rather than elongated tails (see Fig. 1, ref. 1).

outcome (rather than simply the rate) of agonistic interactions, particularly during territory establishment. Finally, the far-reaching consequences of tail asymmetry mean that insofar as female choice does determine male mating success, asymmetrical males may be discriminated against through a female preference for some general aspect of male athleticism, rather than tail symmetry *per se*. Thus while the adaptive importance of tail symmetry is evident^{1,3,4}, the nature of the selective pressures favouring symmetry remain unresolved.

Andrew Balmford
Adrian Thomas
*Department of Zoology,
 Cambridge University, Downing St,
 Cambridge CB2 3EJ, UK*

SIR — We question Møller's claim¹ that female barn swallows use male tail feather asymmetry as an indicator of genetic quality. He offers no direct support for this hypothesis. A likely function for elongated, symmetrical male tail feathers is that they indicate male experience and females use them to assess potential male parenting ability. Previously, Møller showed that male tail length correlates strongly with arrival date and age⁷,

which reflects experience, and that male barn swallows feed nestlings as much as or more than females⁵. Therefore, differences among males in ability to give care should influence female mating decisions. Møller now offers nonsignificant differences in offspring tarsus length and body weight among treatments as evidence against the hypothesis that tail length and symmetry affect foraging ability. This test fails to address the possibility that females use male tail feathers to predict parenting ability, and that differences in male parental care between treatments influence number, rather than size, of young fledged. To exclude nongenetic benefits to choosy females, unmanipulated tail feather length and symmetry must not correlate with male ability to provision and fledge young.

Møller's new results also contain several inconsistencies. Of particular concern are the small standard errors reported for pre-mating period and egg-laying date in each treatment compared with two earlier experiments on barn swallows^{8,9} that replicate the two asymmetry controls in which Møller¹ shortened or elongated tail feathers but did not alter their symmetry. For example, the pre-mating period for the shortened asymmetry control has a standard error only 7% of that reported previously⁸, despite similar sample sizes. Further, the two asymmetry controls do not contain sufficient unexplained variation to account for the effects of the treatments where both length and asymmetry were altered.

Møller states that all males within each treatment, including those with shortened tails and experimentally enhanced asymmetry, mate¹. This is at odds with his earlier 3-year study in which 33% of males with short tails failed to mate⁷. If females discriminate against asymmetric, short-tailed males, then more of the extreme experimental males should go unmated than unmanipulated males.

The experimental treatments altering tail feather asymmetry and length explain nearly all the variation in pre-mating period and egg-laying date. With such small errors within and large differences between treatments, we question how Møller could have assigned males at random to treatments as he states. The sample sizes he reports are not consistent with simultaneously assigning males to treatments in octets. If males were assigned to groups in order of arrival, then this could account for the low variation and contribute to differences between treatments.

Gerald Borgia
Gerald Wilkinson
 Department of Zoology,
 University of Maryland,
 College Park, Maryland 20742, USA

MØLLER REPLIES — Balmford and Thomas suggest that ornamental symmetry may have evolved and been maintained primarily under natural selection. This may not be particularly likely because the primary reason for the increased level of asymmetry and the pattern of asymmetry in secondary sexual characters is obviously sexual selection. They suggest that asymmetry may have a substantial direct fitness effect on females by affecting male food provisioning. Contrary to what one perhaps should expect, the most preferred males feed their nestlings less than the least preferred males¹⁰. In other words, females work harder if they have acquired a preferred male. This was also the case in the asymmetry experiment (A.P.M., manuscript submitted), and there is no net effect on offspring size because females compensate for their mates. The relationship between female parental care and male ornament size is a direct causal relationship as demonstrated by a tail manipulation experiment performed after mate acquisition (de Lope and Møller, manuscript submitted).

Balmford and Thomas also suggest that the effects of the experiment may have arisen due to male combat rather than female choice. I dismissed this possibility¹ although I gave no data for reasons of brevity. There is clearly no effect on male fighting. The frequency of fights is very high, and the sampling periods are of a sufficient duration as determined by repeatability and consistency analyses. The outcome of male fights was not considered because males almost always win (in more than 99% of cases) when fighting within their own territory due to site related dominance.

Borgia and Wilkinson suggest that females may have chosen males with symmetric and long tails for the direct fitness benefits. Males do provide a lot of parental care, but this cannot be the reason for female mate preferences. Females mated to preferred males provide relatively more, not relatively less care¹⁰. There is a direct (negative) causal relationship between parental care and male ornament size because a tail length experiment performed after mate acquisition demonstrated that females mated to males which suddenly had elongated tails provided relatively more parental care (de Lope and Møller, manuscript submitted).

Borgia and Wilkinson further suggest that the standard errors are only 7% of those reported from a previous experiment, but the previously reported data contained standard deviations, not standard errors. They also claim that the two treatments that retained natural asymmetry did not show greater unexplained variation than the treatments where both

length and asymmetry were changed. This is not the case because these explained 3 and 7% less of the variance. A larger fraction of males could not be unmated because there is a large between-year variation in the percentage unmated males which ranges from 2 to 25%, on average 12.5% (ref. 11). The percentage unmated males in 1991 was in fact very low, only 2%.

Finally, the sample sizes are claimed not to be consistent with simultaneous assignment of males to octets. A total of 12 complete octets were created since octet number 13 was only partly filled because no more unmated birds were available. Four birds were never resighted again after release. Males were not assigned to treatment groups in order of arrival since arrival date was unrelated to treatment ($F = 0.16$, d.f. = 7, 86, $P = 0.99$).

A. P. Møller
 Department of Zoology,
 Uppsala University,
 Box 561,
 S-751 22 Uppsala,
 Sweden

1. Møller, A. P. *Nature* **357**, 238–240 (1992).
2. Parsons, P. A. *Biol. Rev.* **65**, 131–145 (1990).
3. Thomas, A. *Phil. Trans. R. Soc.* (in the press).
4. Møller, A. P. *Proc. R. Soc. Lond.* **B243**, 59–62 (1991).
5. Møller, A. P. *Nature* **339**, 132–135 (1989).
6. Møller, A. P. & Höglund, J. *Proc. R. Soc. Lond.* **B245**, 1–5 (1991).
7. Møller, A. P. *Anim. Behav.* **39**, 458–465 (1990).
8. Møller, A. P. *Nature* **332**, 640–642 (1988).
9. Smith, H. & Montgomerie, R. *Behav. Ecol. Sociobiol.* **28**, 195–201 (1991).
10. Møller, A. P. *J. evol. Biol.* (in the press).
11. Møller, A. P. *J. anim. Ecol.* **58**, 1051–1063 (1989).

Confusion of kingdoms

SIR — Field biologists are not the intended audience for most of the advertising appearing in *Nature*, but the illustrations occasionally draw our attention. Not always with the desired effect, however. In your 21 May 1992 issue, below a photograph of several gorgonians, we learn that "To produce the highest quality agarose, it is essential to begin with the best seaweed. . .".

Marine invertebrates comprise or dominate more than 3/4 of the 30-plus phyla of multicellular animals currently extant; J. Mann in *News and Views* (*Nature* **358**, 540; 1992) outlines their considerable importance in natural products research. Yet how many biologists can identify these creatures to phylum or even kingdom? Not enough apparently.

Nancy Knowlton
 Smithsonian Tropical Research
 Institute,
 Apartado 2072,
 Balboa, Republic of Panama
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