

product particles are not dense, as they would be if grown by accretion from solution, but are porous and of high surface area. Tiny nuclei of silica, ~ 4 nm in-diameter, agglomerate to form remarkably uniform spherical clusters of diameter 159 nm. Using the relevant values¹⁴ in equation (4) ($E = 7 \times 10^{10}$ Pa, $\gamma_{SL} = 0.03 \text{ J m}^{-2}$, $\nu = 0.3$) predicts a dominant cluster size of 145 nm, close to the experimental value. We have found that large clusters form in silica sols after colloidal destabilization with salt²³.

Growth of clusters was also observed in dispersions of polymer particles. Amorphous monosize spherical particles of polystyrene ($D = 0.244 \text{ }\mu\text{m}$, $E = 2.5 \times 10^9$ Pa, $\gamma_{SL} = 0.04 \text{ J m}^{-2}$, $\nu = 0.3$) (provided by E. Jones of ICI Colloid Science Group) were suspended in water and gave the particle size distribution shown in Fig. 3c. After destabilizing with aluminium chloride solution, however, flocculation occurred and a large cluster eventually emerged (Fig. 3d) with a mean size of $8 \text{ }\mu\text{m}$, comparable with the value of $10.3 \text{ }\mu\text{m}$ predicted from equation (4). Previous studies of flocculation in latex dispersions have not reported this clustering²⁴, although in general experimental conditions such as pH may be important. It has long been suspected that emulsion polymerization of styrene and other monomers proceeds by nucleation followed by coagulation to form monosize latex particles²⁵⁻²⁷. Large latex spheres, when studied by electron microscopy, are seen to comprise many smaller spheres stuck together.

Thus, flocculation of colloidal suspensions leads to the self-assembly of rounded, close-packed clusters, predominantly of a specific size, which are orders of magnitude larger than the primary particles. This phenomenon demonstrates how weak colloidal forces acting between fine particles can control the structure and strength of the strongest ceramic solids. Paradoxically, the weaker the van der Waals attraction, that is, the lower the interfacial energy γ_{SL} , the larger are the clusters and the weaker the ceramic as a consequence of these large flaws. Obviously, this argument is only true if the clusters are sufficiently strong to resist breakdown during the ceramic mixing and moulding process²⁸⁻³⁰. The ultimate in weak colloidal forces obtains in biological systems^{31,32} where the surface energy of cells may be as low as 1 mJ m^{-2} . In this case large cellular clusters, of the order of a few millimetres in diameter, are predicted by equation (4). Such clustering may play a part in biological growth processes. |

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1. Davidge, R. W. & Tappin, G. J. *Mater. Sci.* **3**, 165-173 (1968)
2. Davidge, R. W. & Evans, A. G. *Mater. Sci. Engng* **8**, 281-298 (1970)
3. Lange, F. F. *J. Am. Ceram. Soc.* **68**, 396-398 (1983)
4. Lange, F. F. & Metcalf, M. J. *Am. Ceram. Soc.* **68**, 398-406 (1983)
5. Lange, F. F., David, B. I. & Aksay, I. A. *J. Am. Ceram. Soc.* **68**, 407-408 (1983)
6. Alford, N. McN., Birchall, J. D. & Kendall, K. *Nature* **330**, 51-53 (1987)
7. Alford, N. McN., Kendall, K., Clegg, W. J. & Birchall, J. D. *Adv. Ceram. Mater.* **3**, 113-117 (1988)
8. Griffith, A. A. *Phil. Trans. R. Soc. Lond.* **A221**, 163-198 (1920)
9. Zettlemoyer, A. C. (ed.) *Nucleation Phenomena* Vol. 7 (Elsevier, New York 1977).
10. Larson, M. A. & Garside, J. J. *J. Chem. Engng Sci.* **41**, 1285-1290 (1986)
11. Binder, K. & Stauffer, D. *Adv. Phys.* **5**, 343-396 (1976)
12. Hoare, M. R. Pal, P. & Wegener, P. P. *J. Colloid Interface Sci.* **75**, 126-137 (1980)
13. Johnson, K. L., Kendall, K. & Roberts, A. D. *Proc. R. Soc. Lond.* **A324**, 301-313 (1971)
14. Kendall, K. & Padgett, J. C. *Int. J. Adhesion Adhesives* **2**, 149-154 (1982)
15. Kendall, K., Alford, N. McN. & Birchall, J. D. *Spec. Ceram.* **8**, 255-265 (1986)
16. Kendall, K., Alford, N. McN. & Birchall, J. D. *Nature* **325**, 794-796 (1987)
17. European Patent Publ. no. 0288208 (1988)
18. Santacesaria, E., Tonello, M., Storti, G., Pace, R. C. & Carra, S. *J. Colloid Interface Sci.* **111**, 44-53 (1986)
19. Strickland-Constable, R. F. *Kinetics and Mechanism of Crystallisation* (Academic Press, New York, 1968)
20. Wilcox, W. R. *J. Cryst. Growth* **65**, 133-142 (1983)
21. Stober, W., Fink, A. & Bohn, E. *J. Colloid Interface Sci.* **26**, 62-66 (1968)
22. Bogush, G. H. & Zuboski, C. F. *Conf. Proc. on Microstructures '86* Berkeley, California (1986)
23. Martin, J. E. *Phys. Rev.* **A36**, 3415-3341 (1987)
24. Cornell, R. M., Goodwin, J. W. & Ottewill, R. H. *J. Colloid Interface Sci.* **71**, 254-266 (1979)
25. Feeney, P. J., Geissler, E., Gilbert, P. G. & Napper, D. H. *J. Colloid Interface Sci.* **121**, 508-513 (1988)
26. Fitch, R. M. & Watson, R. C. *J. Colloid Interface Sci.* **68**, 14-20 (1979)
27. Fitch, R. M. *Brit. Polymer J.* **5**, 467-469 (1973)
28. Kendall, K. *Powder Met.* **31**, 28-31 (1988)
29. Kendall, K. *Br. Ceram. Proc.* (in the press)
30. Kendall, K. *Powder Technol.* (in the press)
31. Weiss, L. *The Cell Periphery, Metastasis and other Contact Phenomena* Ch 5 (North Holland, Amsterdam, 1967)
32. Ruckenstein, E. & Gourisankar, S. V. *J. Colloid Interface Sci.* **101**, 436-451 (1984)

Viability costs of male tail ornaments in a swallow

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MALE sexual ornaments that increase mating success may evolve even when they decrease other components of fitness such as survival¹⁻⁹. But natural covariation between the apparent level of investment in such ornaments and fitness components such as mating success, fecundity and survival, does not provide incontrovertible evidence that the ornaments are costly, because uncontrolled variables such as overall health⁹ may affect several components of fitness at the same time¹⁰⁻¹². By experimental manipulation of male tail length in the monogamous swallow, *Hirundo rustica*, however, the effects of tail endowment can be tested directly. I show here that in such experiments, females prefer males with elongated tails over those with shortened tails¹³, but that males with experimentally elongated tail ornaments captured smaller, less profitable prey than those with shortened tails. Impaired foraging efficiency of tail-elongated males increased the frequency of fault bars in their tail feathers, probably as a result of food deficiency during moult. Males with experimentally elongated tail ornaments also decreased their natural tail size during moult, thereby causing a fitness loss in terms of delayed breeding and a reduced annual production of offspring resulting from reduced sexual attractiveness during the following year.

The swallow is a monogamous insectivorous passerine of about 20 g in body weight, which forages on the wing and nests in colonies ranging from 1 to 38 pairs in the area studied, at Kraghede, Denmark^{13,14}. Experimental manipulation of male tail length has previously been found to affect the mating success of swallows: females reject males with shortened tails, and experimentally tail-shortened males have longer pre-mating periods¹³. Males with elongated tails acquired mates which laid earlier and produced second clutches more frequently than mates of tail-shortened swallows¹³. Annual reproductive success of males therefore increases with increasing length of their experimentally manipulated tails. Male swallows with elongated tails were also preferred over other males as extra-pair copulation partners¹³. As male swallows with long tail ornaments are preferred by females, further enlargement of this trait must be counteracted by some kind of cost.

To investigate the presence and the extent of such cost experimentally, I manipulated tail length of male swallows during the 1987 breeding season¹³. Male birds were caught at night when they were roosting in their breeding territories, and assigned randomly to one of four groups. The first group (shortened) had a 20 mm piece of feather cut from the middle of the two outermost tail feathers (from 20 mm from the feather base). Apical pieces were glued back using cyanoacrylate 'Superglue' and liquid self-cure acrylic repair material as a catalyst. Mean tail length in this group was reduced by 19.6% to 84 mm. The second group of males (elongated) had the 20 mm pieces inserted into the middle of their outermost tail feathers (20 mm from the base), resulting in an average increase of 16.4% to 125 mm. The third group of male swallows (control group I) had their outermost tail feathers cut in a similar way and the pieces glued back again to control for treatment effects. Mean tail length of this group was reduced by 1% to 103 mm. The fourth group of birds (control group II) were caught and released again without any tail treatment. Mean tail length of this group was 103 mm. The range of manipulated tail lengths (74-138 mm) was very similar to the natural range in the population (84-132 mm; $N = 522$). A total of 44 males were captured shortly after arrival and before acquisition of a mate, whereas 39 males were captured shortly after mating. Swallows from these two groups did

not differ significantly ($P > 0.20$) in any of the analyses of this paper. I collected additional data on ornament size in swallows in the Kraghede study site during 1984-88.

Swallows feed mainly on dipteran prey during the breeding season, and prefer large prey items over small ones^{15,16}. Large diptera are strong flyers which deftly evade capture attempts by swallows¹⁷. Tail size might therefore be an optimum for efficient prey capture by individuals of a particular body size and condition. Alternatively, swallows might exhibit tails of longer than optimal size, with which they are able to capture prey with reduced but still adequate efficiency. I tested these hypotheses by collecting food brought during calm weather from 09:00 to 12:00 hours to first brood nestlings aged 8-12 days and by recording feeding visits during a one-hour daily observation

period of each pair (up to eight pairs could be watched simultaneously). Nestlings were fitted with neck collars¹⁸ to prevent them from swallowing the food boluses brought to them by their parents. The boluses contained 1-155 insects with 15 insects the average. This sampling procedure did not affect the size of prey brought to nestlings¹⁹. After each visit I removed the bolus from the offspring and recorded the identity of the parent bringing the food. I collected from four to eleven boluses brought by each parent, in total 362 boluses, which were preserved in alcohol. The length of 5,593 prey items was later measured to the nearest 0.1 mm under a light microscope, and body weight was estimated from these body lengths²⁰. Median size of prey brought by parent swallows to their offspring differed among groups of males with different tail-manipulations ($F = 4.43$;

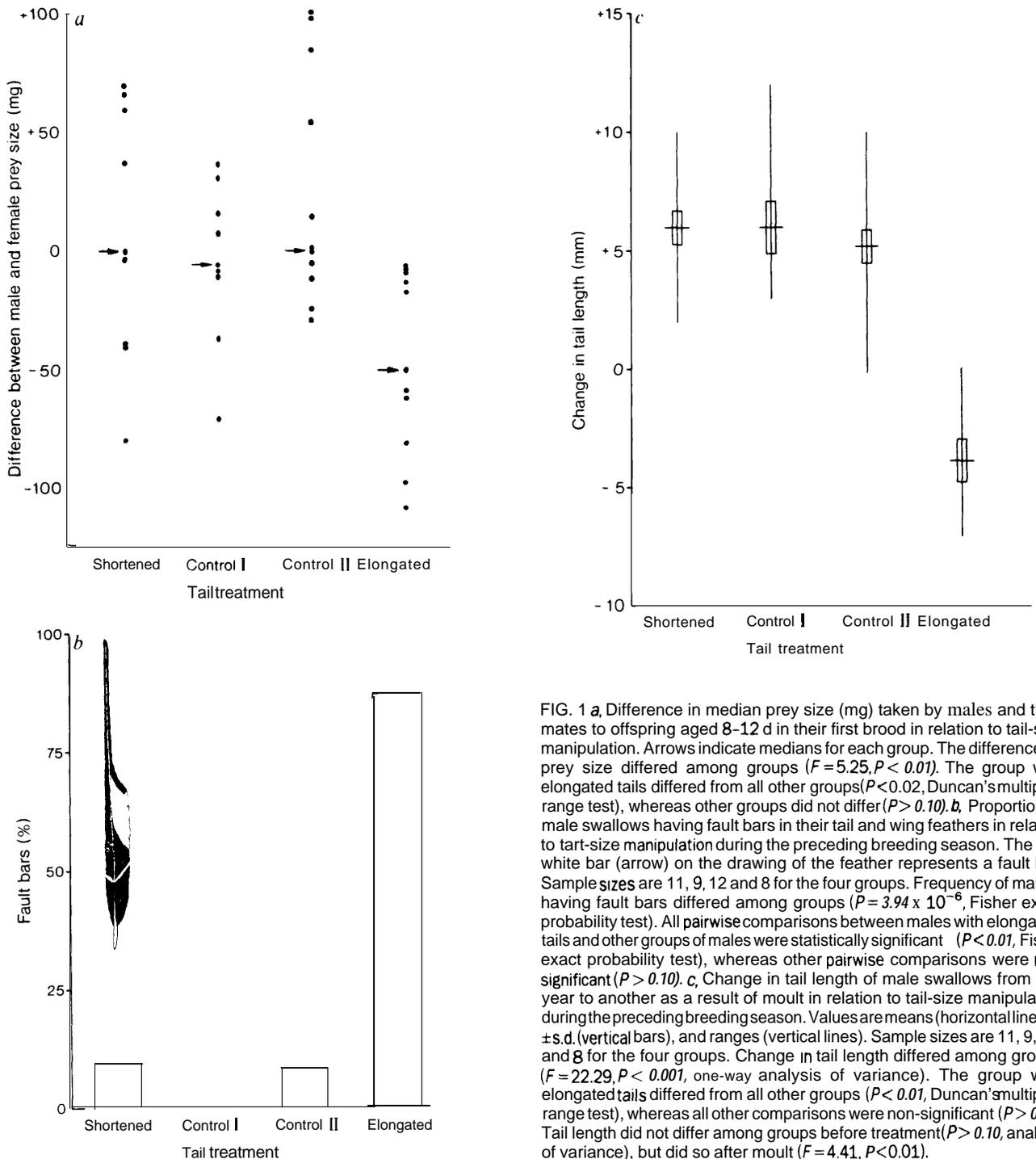


FIG. 1 **a**, Difference in median prey size (mg) taken by males and their mates to offspring aged 8-12 d in their first brood in relation to tail-size manipulation. Arrows indicate medians for each group. The difference in prey size differed among groups ($F = 5.25, P < 0.01$). The group with elongated tails differed from all other groups ($P < 0.02$, Duncan's multiple-range test), whereas other groups did not differ ($P > 0.10$). **b**, Proportion of male swallows having fault bars in their tail and wing feathers in relation to tail-size manipulation during the preceding breeding season. The thin white bar (arrow) on the drawing of the feather represents a fault bar. Sample sizes are 11, 9, 12 and 8 for the four groups. Frequency of males having fault bars differed among groups ($P = 3.94 \times 10^{-6}$, Fisher exact probability test). All pairwise comparisons between males with elongated tails and other groups of males were statistically significant ($P < 0.01$, Fisher exact probability test), whereas other pairwise comparisons were non-significant ($P > 0.10$). **c**, Change in tail length of male swallows from one year to another as a result of moult in relation to tail-size manipulation during the preceding breeding season. Values are means (horizontal lines), \pm s.d. (vertical bars), and ranges (vertical lines). Sample sizes are 11, 9, 12 and 8 for the four groups. Change in tail length differed among groups ($F = 22.29, P < 0.001$, one-way analysis of variance). The group with elongated tails differed from all other groups ($P < 0.01$, Duncan's multiple-range test), whereas all other comparisons were non-significant ($P > 0.10$). Tail length did not differ among groups before treatment ($P > 0.10$, analysis of variance), but did so after moult ($F = 4.41, P < 0.01$).

TABLE 1 Effect of tail treatment of male swallows during one breeding season on fitness components during their following season

Fitness component	Tail treatment				(P)
	Shortened	Control I	Control II	Elongated	
Survival rate (%)	50.0	42.9	60.0	40.0	(>0.10)
Duration of pre-mating period (days)	2.6 ^a (2.7)	2.6 ^a (2.0)	2.5 ^a (1.8)	8.5 ^b (6.7)	(<0.01)
Proportion having second clutches (%)	63.6	55.6	58.3	25.0	(>0.10)
Fledglings per male	7.3 ^a (1.6)	7.1 ^a (2.8)	7.3 ^a (2.4)	4.0 ^b (1.9)	(<0.01)
Sample size	11 (22)	9 (21)	12 (20)	8 (20)	

Values are percentages (survival, proportion having second clutches) or means (1 s.d.) (other fitness components). P values calculated from a G-test (survival, proportion of males having second clutches) or from a one-way analysis of variance (other fitness components). Mean values for treatments are significantly different from each other if they have different superscripts (a and b) ($P < 0.05$, Duncan's multiple-range test). Sample sizes are number of survivors and, in parentheses, number of males originally manipulated.

$P \sim 0.01$, one-way analysis of variance). Males with elongated tails brought significantly smaller prey items than all other groups of male swallows ($P < 0.05$, Duncan's multiple-range test).

Females did not differ among male tail-manipulation groups in the size of prey offered to their offspring ($F = 1.10$; $P > 0.30$, one-way analysis of variance). As weather, time of day and time of season all affect the kind of prey available to foraging swallows⁷, the most appropriate comparison is between males and their mates foraging at the same time. Males with elongated tails brought smaller insects than their mates, whereas sexes did not differ in the size of prey taken for any other treatment group (Fig. 1 a). Male swallows with elongated tails were more successful in obtaining extra-pair copulations than others, although males of all four groups attempted such extra-pair copulations at a similar rate¹³. Males with elongated tails may thus have put more effort into trying to get additional mates, rather than providing food for their offspring. However, this is not a plausible alternative explanation because extra-pair copulations exclusively take place during egg-laying and incubation periods of female mates and not during the nestling period⁸.

Male swallows with elongated tails might catch fewer insects than other males if impaired in their foraging ability by the tail manipulation. But males with elongated tails brought more insects per food bolus than other males ($F = 3.60$; $P < 0.05$). They also brought more insects per bolus than their simultaneously foraging mates, although this was not the case for the other groups of males ($F = 6.72$; $P < 0.001$). Median food bolus weight did not differ between experimental groups of males ($F = 1.10$, n.s.), nor did male swallows with elongated tails differ from their mates in median bolus weight more than any other group ($F = 1.26$, n.s.). Mean feeding rate per male swallow during the entire nestling period did not differ between treatments ($F = 0.77$, n.s.), and males with elongated tails did not differ in feeding rate from their mates more than any other experimental group ($F = 0.35$, n.s.). In conclusion, males with elongated tails worked harder than any other group of males.

Swallows moult once a year during a six-month period in their African winter quarters²²⁻²³. If suffering from energy or nutrient deficiency during moult, birds acquire light, so-called fault bars in their feathers, and these sites are especially prone to later breakage²⁴. On average 4.8% ($N = 522$) of the unmanipulated male swallows in my study area were found to possess such fault bars in their tail and wing feathers, short-tailed males more frequently (tail length 86-105 mm: 9.4%; $N = 202$) than males with intermediate and long tails (tail length 106-115 mm: 2.1%; $N = 242$; tail length 116-132 mm: 1.3%; $N = 78$; $G^2 = 13.77$; $P < 0.01$). Tail treatment significantly affected the frequency of fault bars because males with elongated tails were significantly more likely to have bars in 1988, whereas control or tail-shortened males rarely had any (Fig. 1 b).

Although the tail length of a given male swallow in consecutive years is to a certain extent repeatable²⁵ ($r = 0.75$ (s.e. = 0.16); $F = 7.05$; d.f. = 48, 49; $P < 0.001$), in unmanipulated males the

tail length does change between years by between -4 and +18 mm (+4.8 mm on average; 1 s.d. = 4.9; $N = 63$). Long-tailed unmanipulated males increase more in tail length than short-tailed male swallows: the reduced major axis coefficient²⁶ from tail length in year ($i + 1$) regressed on tail length in year (i) was significantly larger than unity (regression coefficient = 1.10 (s.e. = 0.04); $t = 2.66$, d.f. = 61; $P = 0.01$). Experimental manipulation of tail length caused a decrease in pre-manipulation tail size after moult among males with elongated tails, whereas males of all other groups increased the size of their tails (Fig. 1 c).

Tail manipulations of male swallows did not significantly affect survival rates of males (Table 1), although survivors with elongated tails had longer unmanipulated tails than non-survivors (survivors: 114.3 mm, 1 s.d. = 11.3, $N = 8$; non-survivors: 102.3 mm, 1 s.d. = 11.0, $N = 12$, $t = 4.80$, $P < 0.001$). Surviving and non-surviving males did not differ in unmanipulated tail length in any of the other three groups ($P > 0.30$). Long-tailed males were thus better able to carry an elongated tail ornament than short-tailed male swallows.

The size of tail ornaments in male swallows strongly affects, through female choice, subsequent mating and reproductive success¹³. Males with elongated tail feathers during the previous reproductive season had more difficulty in attracting a mate as they experienced significantly longer pre-mating periods than all other males (Table 1). All males in the end did acquire a mate, but females who mated with males with previously elongated tails tended to have second clutches less frequently than other females (Table 1). Annual reproductive success measured as the total number of fledglings produced during both first and second breedings differed significantly among groups, and males with previously elongated tails had significantly reduced reproductive success compared with males from other groups (Table 1). Reduced reproductive success of males with previously elongated tails was probably due to acquisition of mates of inferior non-heritable quality^{1,27,28}, expressed as low double-clutching ability.

Tail ornaments in *H. rustica* appear to be costly traits maintained by female choice. Males breeding for the first time seem to invest heavily in tail growth during moult in order to increase their sexual attractiveness²⁹; they are the only group of males with a high frequency of fault bars in their feathers. The evidence presented here indicates that models of sexual selection should take into account the variation in the male's ability to bear the costs of developing and carrying ornaments, because these differences can apparently give rise to a positive association between the extent of development of the ornament and one or more components of fitness^{7,8,30,31}. □

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1 Fisher, R. A. *The Genetical Theory of Natural Selection* 2nd edn (Dover, New York 1958)

2 Lande R. *Proc natn Acad Sci U.S.A.* **79**, 3721-3725 (1981)

3 Kirkpatrick, M. *Evolution* **36**, 1-12 (1982)

4 Andersson, M. *Biol J Linn Soc* **17**, 375-393 (1982)

5 Andersson M. *Evolution* **40**, 804-816 (1986)

6 Hamilton W. D. & Zuk M. *Science* **218**, 384-387 (1982)

7. Partridge, L. & Endler, J. A. in *Sexual Selection: Testing the Alternatives* (eds Bradbury, J. W. & Andersson, M. B.) 265-277 (Wiley, Chichester, 1987).
8. Pomiankowski, A. *Oxford Surv Evol Biol.* **5**, 136-184 (1988).
9. Seger, J. *Evolution* **39**, 1185-1193 (1985).
10. Partridge, L. & Harvey, P. H. *Nature* **316**, 20-21 (1985).
11. Reznick, D. *Oikos* **44**, 257-267 (1985).
12. Bell, G. & Koufopoulos, V. *Oxford Surv Evol Biol.* **3**, 83-131 (1985).
13. Møller, A. P. *Nature* **332**, 640-642 (1988).
14. Møller, A. P. *Anim. Behav.* **35**, 819-832 (1987).
15. Turner, A. K. thesis, Univ Stirling (1980).
16. Turner, A. K. *Anim Behav* **30**, 862-872 (1982).
17. Waugh, D. R. thesis, Univ Stirling (1978).
18. Orians, G. H. & Horn, H. S. *Ecology* **50**, 930-938 (1969).
19. Henry, C. *Alauda* **50**, 92-107 (1982).
20. Rogers, L. E., Hinds, W. T. & Buschborn, R. L. *Ann Ent.Soc. Am* **69**, 387-389 (1976).
21. Møller, A. P. *Behav Ecol. Sociobiol.* **17**, 401-408 (1985).
22. Broekhuysen, G. J. & Brown, A. R. *Ardea* **51**, 25-43 (1963).
23. Mendelsohn, J. A. *Transvaal Mus.* **28**, 79-89 (1979).
24. Harrison, C. J. O. in *A Dictionary of Birds* (eds Campbell, B. & Lack E.) 472-474 (Poyser, Calton, 1985).
25. Becker, W. A. *Manual of Quantitative Genetics* 4th edn (Academic Enterprises, Pullman, 1984).
26. Sokal, R. R. & Rohlf, F. J. *Biometry* 2nd edn (Freeman, San Francisco, 1981).
27. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (Murray, London, 1871).
28. O'Donald, P. *Nature* **237**, 349-351 (1972).
29. Møller, A. P. *Anim Behav* (in the press).
30. Kirkpatrick, M. *Am. Nat.* **125**, 788-810 (1985).
31. Kirkpatrick, M. *Am Nat.* **127**, 222-240 (1986).

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Disparity curvature and the perception of three-dimensional surfaces

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BINOCULAR stereopsis provides information about the relative distance of objects from the differences in the horizontal position of their images on the two retinas¹⁻³. Because the size of the disparity between two points is inversely related to the square of the viewing distance, it is usually assumed that disparities have to be scaled according to distance using the vergence angle of the eyes, or by using the small vertical disparities that also exist between corresponding points of the two images^{4,5}. Here we present evidence that the visual system could extract information about the shapes of surfaces (without the need for scaling) by using the second spatial derivative of disparity—disparity curvature—which remains invariant with viewing distance⁶. Rather than computing the second derivative, we suggest that an approximation to disparity curvature could be derived from the differences in curvature of corresponding line elements in the two eyes.

How good are human observers at detecting and discriminating curved surfaces, and to what extent is this performance

consistent with the use of mechanisms which compute disparity curvature? In our first experiment, observers were asked to judge whether a horizontally orientated cylindrical surface covered with random dots was convex or concave with respect to the observer, using a forced-choice paradigm. Observers were able to discriminate the direction of surface curvature reliably when the surface had a disparity curvature of less than $0.02 \text{ min deg}^{-2}$, corresponding to a radius of curvature of more than 350 cm at the 57 cm viewing distance. Moreover, the disparity range between the closest and furthest parts of the surface at threshold was only one third of that required to discriminate the direction of surface slant over the same spatial extent⁷.

In a second experiment, observers were asked to judge which of two cylindrical surfaces appeared to have the greater perceived curvature. Discrimination thresholds were measured for surfaces with a 256:1 range of disparity curvatures from 0.14 arc min deg^{-2} (a radius of curvature at the peak of the cylinder of 48.5 cm) to 36 arc min deg^{-2} (radius of curvature of just 0.19 cm). The results show that observers can do the task with considerable precision. The difference in disparity curvature that could be reliably discriminated was between 4-6% of the disparity curvature of the reference surface, over the central range of disparity curvatures (Fig. 2).

In a third experiment, a matching paradigm was used to obtain an estimate of the variability of matched curvature settings. The random-dot reference and test surfaces were presented alternately for 2 s each and observers were required to alter the curvature of the test surface until it appeared to be the same as that of the reference. The standard deviation of the final matched settings was typically 3-4% of the reference disparity curvature and was approximately constant over a wide range of disparity curvatures.

These experiments show that performance at discriminating or matching singly curved surfaces is very good, but is it based on the judgement of surface curvature *per se*, or could there be some other difference between the surfaces which might be responsible for the impressive performance? The parabolic surfaces used in the latter two experiments were terminated in tangential planes which had the same gradient for each of the stimuli in the forced choice series. Hence, observers could not have been using the gradient of the flanking regions as a cue. Second, we found that performance was not impaired when the disparity range of all the forced choice stimuli was kept constant, ruling out the possibility that the discriminations were based on the disparity range of individual stimuli. Finally, we have data from a fourth experiment which show that observers are able to accurately match the perceived curvature of two parabolic surfaces at different distances (57 and 114 cm) from the observer⁸. At the point of a perfect match, the two surfaces had identical object dimensions, which meant that the disparity range of the two surfaces differed by a factor of four and the disparity gradients of the flanking regions differed by a factor of two.

FIG. 1a, The binocular disparity between two points in space is defined as the difference in the vergence angles needed to fixate each of the two points (Disparity = $\beta_1 - \beta_2$). **b**, Disparity gradient^{1,9,20} (dg) is defined as the rate of change of disparity over visual angle (in the limit $(\beta_1 - \beta_2)/\theta$). The disparity difference between a pair of points will be roughly one quarter when the viewing distance is doubled (Disparity $\propto 1/d^2$), but because the angular separation of the two points will be half, $\theta/2$, the disparity gradient will only halve ($\text{dg} \propto 1/d$). **c**, Disparity curvature is defined as the rate of change of disparity gradient over visual angle (in the limit, $\text{dg}_1 - \text{dg}_2/\phi$). Because the disparity gradients of each of a pair of points on a surface will halve with a doubling of viewing distance, and the angular separation between those two points will also halve, the disparity curvature will remain approximately constant.

