

shapes in any one chain, whereas the latter adopt morphologies that can be unique and species-specific¹⁴. The general similarities between the two systems, however, suggests that the biological control mechanisms have much in common.

The biomineralization of bacterial magnetite involves the formation of a transient hydrous Fe(III) oxide precursor, which subsequently transforms to magnetite^{15,16}. The presence of both greigite and iron pyrite in the organism we describe indicates that there could be a similar relationship between the two mineral phases. But under thermodynamic conditions, in a highly reducing environment at neutral pH, greigite would slowly transform to pyrite¹⁷. This implies that unless the organism continues to maintain its capacity to synthesize greigite, it would slowly lose its magnetotactic response. Thus greigite may be a metastable phase in the transformation of an undetected precursor into pyrite. Alternatively, the cells might separately mineralize greigite and pyrite by local control of iron and sulphide concentration, reducing potential and pH.

Structurally, Fe₃S₄ and Fe₃O₄ are isomorphous, both materials adopting the face-centred cubic spinel structure. Whether this structural similarity has relevance to the cellular mechanisms of their synthesis is unclear. In terms of their magnetic properties, the saturation magnetization of greigite is about one-third that of magnetite¹⁸. The permanent magnetic single-domain size range for greigite has not been determined but is probably similar to magnetite, because the magnetic ordering temperatures and magnetic anisotropy constants of the two minerals are similar¹⁸. Thus, the 75-nm biogenic greigite particles are likely to be permanent magnetic single domains and responsible for the magnetotactic response of the intact organism. Organization of these particles into chains would result in a parallel alignment of the individual particle moments along the chain direction, and would give each constituent cell a permanent magnetic dipole moment equal to the sum of the individual particle moments in the chain. The net magnetic dipole moment of the intact organism would then be the vector sum of the moments of the constituent cells.

Finally, we note that greigite has been identified as a source of remanent magnetism in sediments¹⁹. These deposits may be of inorganic origin, biologically mediated by sulphate-reducing micro-organisms or resulting from the diagenesis of bacterial magnetite^{19,20}. We note, however, that the crystal size and shape of sediment greigite is similar to that reported here for bacterial greigite, and therefore propose that biogenic minerals should be considered as a further possible source of remanent magnetism in sulphide-rich sediments. □

Received 18 September; accepted 1 November 1989.

1. Frankel, R. B., Blakemore, R. P. & Wolfe R. S. *Science* **203**, 1355–1356 (1979).
2. Blakemore, R. P. A. *Rev. Microbiol.* **36**, 217–238 (1982).
3. Lowenstam, H. A. & Weiner, S. *On Biomineralization* (Oxford University Press, 1989).
4. Peterson, N., von Döbeneck, T. & Vali, H. *Nature* **320**, 611–615 (1986).
5. Stolz, J. F., Chang, S.-B. R. & Kirschvink, J. L. *Nature* **321**, 849–851 (1986).
6. Blakemore, R. P., Blakemore, N. A., Bazylinski, D. A. & Moench, T. T. *Bergey's Manual of Systematic Bacteriology* Vol. 3 (eds Staley, J. T. et al.) 1882–1889 (Williams and Wilkins, Baltimore, 1989).
7. Farina, M., Lins de Barros, H. G. P., Esquivel, D. M. S. & Danon, J. *Biol. Cell.* **48**, 85–86 (1983).
8. Farina, M., Sollarazano, G. & Viera, G. J. *Proc. Xlth Int. Cong. on Electron Microscopy (Kyoto)* 3369–3370 (1986).
9. Hallberg, R. O. *Stockholm Contr. Geol.* **13**, 35–37 (1965).
10. Hallberg, R. O. N. *Jahrbuch Mineral. Monatshefte* 481–500 (1972).
11. Freke, M. & Tate, D. J. *Biochem. microbiol. technol. Eng.* **3**, 29–39 (1961).
12. Lovely, D. R., Stolz, J. F., Nord, G. L. Jr & Phillips, J. P. *Nature* **330**, 252–254 (1987).
13. Bazylinski, D. A., Frankel, R. B. & Jannasch, H. W. *Nature* **334**, 518–519 (1988).
14. Mann, S. & Frankel, R. B. in *Biomineralization: Chemical and Biochemical Perspectives* (eds Mann, S., Webb, J. & Williams, R. J. P.) 389–426 (VCH, Weinheim, 1989).
15. Frankel, R. B., Papafthymiou, G. C., Blakemore, R. P. & O'Brien, W. D. *Biochim. biophys. Acta* **763**, 147–159 (1983).
16. Mann, S., Frankel, R. B. & Blakemore, R. P. *Nature* **310**, 405–407 (1984).
17. Berner, R. A. *Am. J. Sci.* **265**, 773–785 (1967).
18. Spender, M. R., Coey, J. M. D. & Morrish, A. H. *Can. J. Phys.* **50**, 2313–2326 (1972).
19. Demitrack, A. in *Magnetite Biomineralization and Magnetoreception in Organisms* (eds Kirschvink, J. L., Jones, D. D. & MacFadden, B. J.) 625–645 (Plenum New York, 1985).
20. Morse, J. W., Millero, F. J., Cornwell, J. C. & Rickard, D. *Earth Sci. Revs* **24**, 1–42 (1987).

ACKNOWLEDGEMENTS. We thank A. Garratt-Reed for assistance with the STEM measurements and R. P. Blakemore, F. G. Rogers, H. Lins de Barros and D. Esquivel for discussions. S.M. and N.H.C.S. were supported by the UK Science and Engineering Research Council. R.B.F. was supported by the US National Science Foundation. D.A.B. and H.W.J. were supported by the US National Science Foundation and the Office of Naval Research.

Mammalian sex ratios and variation in costs of rearing sons and daughters

M. Gomendio*, T. H. Clutton-Brock†, S. D. Albon†, F. E. Guinness† & M. J. Simpson*

* Sub-Department of Animal Behaviour, Madingley, Cambridge CB3 8AA, UK

† Large Animal Research Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

IN red deer, the sex ratio of calves at birth (calculated as the proportion of calves born that are male) increases with the dominance rank of the mother^{1,2}, whereas opposite trends exist in several populations of macaques and baboons^{3–7}. Here we show that the subsequent survival and reproductive success of subordinate female red deer is depressed more by rearing sons than by rearing daughters, whereas the subsequent fitness of dominant females is unaffected by the sex of their present offspring. By contrast, among subordinate female macaques, the rearing of daughters has greater costs to the mother's subsequent fitness than does the rearing of sons, although again, no difference in the costs of rearing sons and daughters is found among dominant mothers. These findings indicate that both differences in the relative fitness of sons and daughters and differences in the relative costs of rearing male and female offspring can favour variation in the sex ratio.

It has been suggested^{1,2} that the relationship between maternal rank and the birth sex ratio in red deer could arise because the rank of a mother exerts a stronger effect on the fitness of her sons (who compete intensely for mates) than on the fitness of her daughters. By contrast, among baboons and macaques, the rank of a female could affect the fitness of her daughters more than it affects the fitness of her sons, because daughters inherit their mother's social rank, which affects their breeding success. Sons, on the other hand, disperse to other groups where their rank and reproductive success depend extensively on alliances formed with other males^{6,7}. Here we explore the possibility that the costs of rearing sons and daughters also vary with maternal rank, and that they represent an additional selective pressure involved in the evolution of the sex-ratios which has been previously overlooked.

To determine whether the relative costs of rearing sons and daughters in ungulates and primates vary with maternal rank, we investigated the subsequent survival and reproductive performance of mothers that had raised sons versus daughters in a sample of 283 red deer hinds from the Isle of Rhum, and in a sample of 52 female macaques from the colony at Madingley, Cambridge^{5,10}. In both species, dominance rank was assessed from displacements and aggressive interactions at feeding sites^{5,11}. In red deer we used a within-cohort dominance score that removed the effects of age and scaled continuously from 0 (most subordinate) to 1 (most dominant)². In each macaque social group there were two founder females who had reproduced throughout the history of the colony, and maintained stable dominance ranks. The matriarch of the dominant family was designated as dominant, and the matriarch of the subordinate family was designated as subordinate. The other females were excluded from the analyses.

Both the survival over winter and the fecundity of adult female red deer decline with age (fitted as a quadratic function age + age²), with high rainfall in August–September, and with low winter temperature (mean daily temperature in °C in December–February¹¹). Because individuals in the population did not all breed in the same year, we have fitted terms for these phenotypic and environmental variables in generalized linear models¹² to estimate the probability of the mother's survival or fecundity in

TABLE 1 Effects of dominance and offspring sex in red deer and macaques

| | Red deer | | | | | | Macaques | | |
|---|----------|------------------|----------|----------|-------------------|----------|----------|-------------------|----------|
| | χ^2 | Survival d.f. | <i>P</i> | χ^2 | Fecundity d.f. | <i>P</i> | χ^2 | Fecundity d.f. | <i>P</i> |
| Dominance | 2.0 | 1 | NS | 4.2 | 1 | <0.05 | 8.3 | 1 | <0.01 |
| Sex of offspring | 2.0 | 1 | NS | 2.2 | 1 | NS | 1.6 | 1 | NS |
| Dominance–sex interaction | 5.6 | 1 | <0.02 | 4.0 | 1 | <0.05 | 4.7 | 1 | <0.05 |
| Sex and dominance–sex interaction | 7.6 | 2 | <0.05 | 6.2 | 2 | <0.05 | 6.3 | 2 | <0.05 |
| Dominance and sex and dominance–sex interaction | 9.6 | 3 | <0.05 | 10.4 | 3 | <0.02 | 14.6 | 3 | <0.01 |

Goodness-of-fit tests for each of the variables dominance, offspring sex and dominance–offspring sex interaction fitted in the logistic regression models (see Fig. 1) of the probability of over-winter survival and fecundity next summer in female red deer, and the probability of fecundity next year in macaques. Because the dependent variables were binary (survive, 1; die, 0; fecund, 1; not-fecund, 0) and the errors were not normally distributed least-squares regression and analysis-of-variance (ANOVA) techniques were inappropriate. Simple contingency table analysis was also inappropriate because dominance rank among deer was a metric (continuous) variable. Binary data must be related to any metric variable in a nonlinear way. The logistic regression model used here is a form of generalized linear model using a logit link function and binomial error distribution. These models permit the inclusion of significant covariates and therefore, the control of potentially confounding variables. Differences in deviance (analogous to sums of squares in ANOVA) between two models, one with and one without the test variable (for example, sex), are distributed as χ^2 with the appropriate degrees of freedom (d.f.) of the test variables. NS, not significant.

relation to her dominance rank and the sex of her offspring raised through the previous summer.

After controlling for variation due to age, August–September rainfall and winter temperature, over-winter survival in adult female deer was not related to either dominance ($\chi^2 = 2.0$, not significant) or the sex of the offspring ($\chi^2 = 2.0$, not significant), when each was added to the model separately, or together (Table 1). This was because of a significant interaction between dominance and the sex of the offspring (Table 1). Subordinate mothers that had reared male offspring showed low over-winter survival compared with dominant mothers that had reared sons (Fig. 1a). By contrast, among individuals that had produced female offspring, subordinate mothers had the same, or slightly higher, probability of survival compared with dominant mothers (Fig. 1a).

If an adult female red deer survived the winter, the probability of her calving the next summer was influenced by her dominance ($\chi^2 = 4.2$, $P < 0.05$), but not by the sex of her previous offspring ($\chi^2 = 2.2$, not significant). But as with the analysis of survival, there was a significant interaction between dominance and sex (Table 1): subordinate mothers were less likely to calve again after rearing a male offspring the previous summer than they were after rearing a female offspring. Dominant mothers were more likely to calve again than were subordinate mothers, but

the sex of the previous calf seemed to have little influence (Fig. 1b). The extra fitness costs of rearing sons versus daughters seem to be substantial among subordinate mothers but absent among dominant mothers.

Contrasting differences were found in macaques. Subordinate mothers were less likely to breed again the next year than were dominant mothers ($\chi^2 = 8.3$, $P < 0.01$). The interaction with sex (Table 1) was reversed: subordinate mothers were more likely to give birth the following season after rearing a male offspring than they were after rearing a female offspring, whereas dominant mothers were slightly more likely to give birth the following season after rearing a female offspring than after rearing a male offspring (Table 2).

The mechanisms responsible for interactions between maternal rank and the costs of rearing sons and daughters may be

FIG. 1 Logistic curves illustrating the probability of female red deer surviving a winter (a) and calving in the year after rearing a son versus a daughter (b), plotted against their dominance score. Logistic regressions¹³ were of the form:

$$\text{Probability } (Y_1 = 1) = \frac{\exp G(X_1)}{1 + \exp G(X_1)}$$

where $G(X_1) = (A + B_1x_{11} + B_2x_{12} + B_3x_{13} \dots + B_7x_{17})$ and A, B_1, B_2, \dots, B_7 are constants, x_{11} is dominance rank, x_{12} is offspring sex, x_{13} is dominance–sex interaction, x_{14} is age, x_{15} is age², x_{16} is August–September rainfall (mm), x_{17} is mean daily temperature (°C) December–February, and $i = 1, 2, 3, \dots, N$ hind-years. Curves in (a) are standardized for age (12 years), August–September rainfall (750 mm) and December–February mean daily temperature (4 °C). Coefficients in the exponential equation (see above) are—males: $B_1 = 1.573$, $B_2 = 0$, $B_3 = 0$; females: $B_1 = 1.573$, $B_2 = 1.615$, $B_3 = -2.236$; both sexes have the same values for coefficients A (0.73), B_4 (0.383), B_5 (−0.0347), B_6 (−0.003572), and B_7 (0.504). Curves in (b) are standardized for age (12 years), August–September rainfall (750 mm), and December–February mean daily temperature (4 °C). Coefficients in the exponential equation (see above) are—males: $B_1 = 0.526$, $B_2 = 0$, $B_3 = 0$; females: $B_1 = 0.526$, $B_2 = 0.476$, $B_3 = -0.580$; both sexes have the same values for coefficients A (−5.070), B_4 (0.916), B_5 (−0.04746), B_6 (−0.003087), and B_7 (0.5681).

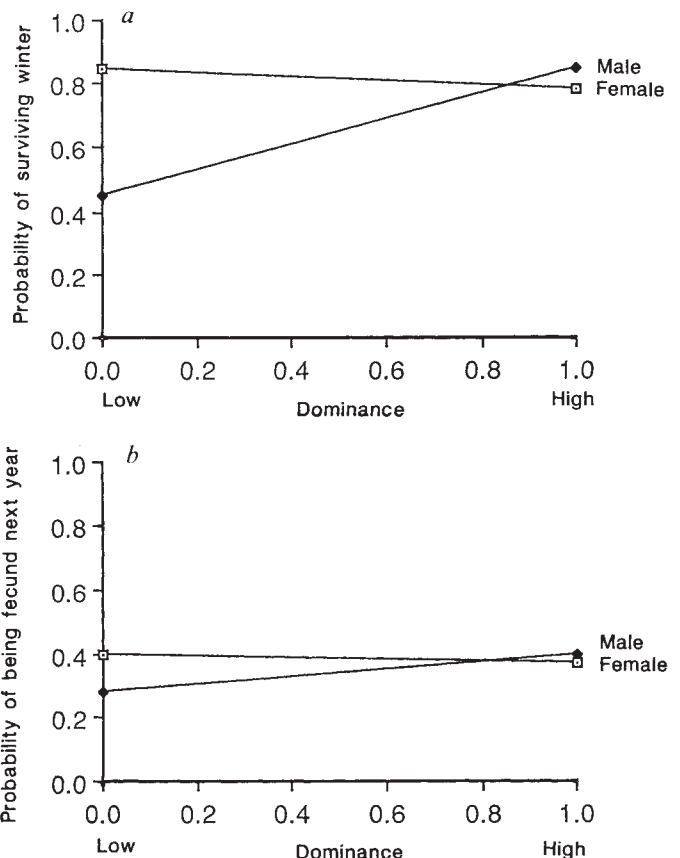


TABLE 2 Probability of fecundity in macaques

| | Male reared | Female reared |
|---------------|-------------|---------------|
| Mother's rank | | |
| Dominant | 0.80 (5) | 0.92 (14) |
| Subordinate | 0.62 (8) | 0.00 (4) |

Probability of subordinate and dominant macaques giving birth the year after rearing sons versus daughters. Number of births sampled are given in parentheses. The generalized linear model for macaques only incorporated the variables dominance, sex, and dominance-sex interaction (see Table 1).

quite different in ungulates and primates. In red deer, goats, and bison, as well as in African elephants^{9,14,15}, sons are suckled more frequently than are daughters during the peak period of lactation and the energetic costs of rearing males probably exceed those of rearing females⁹. Subordinate females could be more strongly affected by these differences because they do not have priority of access to the best feeding sites, and because their body condition is generally poorer than that of dominant females¹⁰. By contrast, no overall differences in suckling were found between male and female infants in rhesus macaques. But, when the interaction between infant sex and maternal rank was examined, it was found that daughters of subordinate mothers tended to be suckled more frequently than their sons, and more than the infants of dominant mothers⁵. Allowing frequent access to the nipple could have been a maternal response to the high levels of aggression and harassment that the daughters of subordinate mothers tended to receive from unrelated females, a phenomenon which has been documented in several studies^{7,16}. Frequent nipple stimulation inhibits ovulation in mammals¹⁷, and this could have been responsible for the longer delays before the next conception among subordinate females that had reared daughters^{5,18}.

Consequently, the results presented here indicate that two separate selection pressures can favour the evolution of the contrasting sex-ratios in ungulates^{1,19-21} and cercopithecine primates³⁻⁷. First, maternal rank can have opposite effects on the relative fitness of sons and daughters^{1,2,6,7}. Second, maternal rank can modify the relative costs of rearing sons and daughters, favouring the production of daughters by subordinate mothers in red deer, and the production of sons by subordinate mothers in macaques. In both cases, these biases could favour the production of an excess of the other sex by dominant females²². □

Received 20 July; accepted 27 November 1989.

- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. *Nature* **308**, 358-360 (1984).
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. *Anim. Behav.* **34**, 460-461 (1986).
- Simpson, M. J. A., Simpson, A. E., Hooley, J. & Zunz, M. *Nature* **290**, 49-51 (1981).
- Simpson, M. J. A. & Simpson, A. E. *Nature* **300**, 440-441 (1982).
- Gomendio, M. thesis, Univ. Cambridge (1988).
- Altman, J. *Baboon Mothers and Infants* (Harvard University Press, 1980).
- Silk, J. B. *Am. Nat.* **121**, 56-66 (1983).
- Ritchie, M. *Am. Nat.* (in the press).
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. *Nature* **289**, 487-489 (1981).
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. *Red Deer: Behaviour and Ecology of Two Sexes* (University of Chicago Press, 1982).
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. *Nature* **337**, 260-262 (1989).
- McCullough, P. & Nelder, J. A. *Generalized Linear Models* (Chapman & Hall, London, 1983).
- Cox, D. R. *The Analysis of Binary Data* (Methuen, London, 1970).
- Pickering, S. P. C. thesis, Univ. Durham (1983).
- Lee, P. C. and Moss, C. J. *Behav. Ecol. Sociobiol.* **18**, 353-361 (1986).
- Dittus, W. P. J. *Behaviour* **69**, 265-302 (1979).
- McNeilly, A. S. in *The Physiology of Reproduction* (eds Knobil, E. & Neill, J.) 2323-2349 (Raven, New York, 1988).
- Gomendio, M. *J. Zool.* **217**, 449-467 (1989).
- Wolff, J. O. *Behav. Ecol. Sociobiol.* **23**, 127-133 (1988).
- Dhillon, J. S., Acharya, R. M., Tiwana, M. S. & Aggarwal, S. C. *Anim. Prod.* **12**, 81-87 (1970).
- Singh, O. N., Singh, R. N. & Srivastava, R. R. P. *Ind. J. vet. Sci.* **35**, 245-248 (1965).
- Fisher, R. A. *The Genetical Theory of Natural Selection* (Oxford University Press, 1930).

ACKNOWLEDGEMENTS. We thank Robert Hinde and Pat Bateson for providing facilities at Madingley, the MRC for access to the macaque colony, the director of the Nature Conservancy Council (Scotland) and the staff of the NCC for permission to work on Rhum, and all those who have helped on the Rhum red deer project for assistance with collecting data on reproductive success and survival. The research was funded by NERC, SERC, the Royal Society, St John's College and Trinity Hall.

A network that learns to recognize three-dimensional objects

T. Poggio & S. Edelman

Artificial Intelligence Laboratory, Center for Biological Information Processing, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA

THE visual recognition of three-dimensional (3-D) objects on the basis of their shape poses at least two difficult problems. First, there is the problem of variable illumination, which can be addressed by working with relatively stable features such as intensity edges rather than the raw intensity images^{1,2}. Second, there is the problem of the initially unknown pose of the object relative to the viewer. In one approach to this problem, a hypothesis is first made about the viewpoint, then the appearance of a model object from such a viewpoint is computed and compared with the actual image³⁻⁷. Such recognition schemes generally employ 3-D models of objects, but the automatic learning of 3-D models is itself a difficult problem^{8,9}. To address this problem in computational vision, we have developed a scheme, based on the theory of approximation of multivariate functions, that learns from a small set of perspective views a function mapping any viewpoint to a standard view. A network equivalent to this scheme will thus 'recognize' the object on which it was trained from any viewpoint.

Is the need for 3-D range-based or manually specified models real? Structure from motion theorems^{10,11}, pioneered by Ullman¹², indicate that full information about the 3-D structure of an object represented as a set of feature points (at least five to eight) is present in just two of their perspective views, provided that corresponding points are identified in each view. A view is represented as a $2N$ vector $x_1, y_1, x_2, y_2, \dots, x_N, y_N$ of the coordinates on the image plane of N labelled and visible feature points on the object. Here, and in most of the following, we assume that all features are visible, as they are in wire-frame objects. The generalization to opaque objects follows by partitioning the viewpoint space for each object into a set of 'aspects'¹³, corresponding to stable clusters of visible features. In principle, therefore, having enough 2-D views of an object is equivalent to having its 3-D structure specified.

This line of reasoning, together with properties of perspective projection, indicate (1) that for each object there exists a smooth function mapping any perspective view into a 'standard' view of the object, and (2) that this multivariate function can be synthesized, or at least approximated, from a small number of views of the object. Such a function would be object-specific, with different functions corresponding to different 3-D objects. Furthermore, the application of the function that is specific for one object to the views of a different object is expected to result in a 'wrong' standard view that can be easily detected as such.

Synthesizing an approximation to a function from a small number of sparse data—the views—can be considered as learning an input-output mapping from a set of examples^{14,15}. A powerful scheme for the approximation of smooth functions has been recently proposed under the name of Generalized Radial Basis Functions (GRBFs), and shown^{14,15} to be equivalent to standard regularization^{16,17} and generalized splines (ref. 14; see closely related work by Powell¹⁸, and Broomhead and Lowe¹⁹). The approximation of $f: R^n \rightarrow R$ is given by

$$f(\mathbf{x}) = \sum_{\alpha=1}^K c_{\alpha} G(\|\mathbf{x} - \mathbf{t}_{\alpha}\|) \quad (1)$$

where the K coefficients c_{α} and the centres \mathbf{t}_{α} are found during the learning stage and G is an appropriate basis function (see refs 14 and 15), such as the gaussian function. A polynomial form of the form $\sum_i d_i p_i(\mathbf{x})$ can be added to the right-hand side of equation (1). In this paper we omit the polynomial term (see