

of burrows in high and low sulphide treatments provide further evidence for chemosensory abilities.

In thyasirids and lucinids, the foot consists of an outer layer of longitudinal and circular muscles, surrounding and traversing a spongy haemocoel⁸. The mechanism of foot extension in thyasirids is likely to have a hydrostatic component, with haemolymph being pumped by the heart from the body mass to the foot (the Keber valve stops haemolymph from returning to the heart¹²), resulting in an increase in foot length provided that the diameter of the foot remains constant or is reduced. Hydrostatic extension, although common in burrowing marine invertebrates, has not been reported to cause such a remarkable increase in length as seen in chemosymbiotic thyasirids (30 times the contracted length). Fully extended, the foot of a chemosymbiotic thyasirid must have an extremely thin, stretched-out epithelium and muscle layer. In this state, sulphide from pore water surrounding the burrow could easily diffuse to the haemal space of the foot. Then, sulphide could be transported to the gills and symbionts when the foot is retracted within the mantle cavity. Transport of sulphide from the foot to the gills has previously been proposed for the chemosymbiotic bivalves *Calyptogena magnifica* and *Calyptogena elongata*^{13,14}.

The sulphide mining behaviour could have been derived from the use of the foot in anterior inhalant tube formation, characteristic of Lucinaceans (lucinids, thyasirids and unguinids)⁸. On X-radiographs of the non-chemosymbiotic unguinid *Diplo donta notata*, some burrows are directed towards the sediment surface, whereas others lead deeper into the sediment, apparently having been misdirected¹⁵. Such accidental burrowing could have evolved into sulphide mining in chemosymbiotic thyasirids and lucinids, as it brought them in contact with pockets of sulphide.

Sulphide mining in thyasirids is not only a recent phenomenon: a fossilized thyasirid from the Middle Miocene, with a tunnel underneath measuring 15 times the shell length, has been discovered in Lower Austria¹⁶. The burrowing behaviour of thyasirids seems to have appeared early in the evolution of the family, whose fossil record goes back to the Cretaceous period¹⁷. Given the lack of a rigorous thyasirid phylogeny, the relationship between symbiotic and non-symbiotic thyasirids, and their relative order of appearance, are unclear. However, if sulphide mining existed in early thyasirids, then non-symbiotic thyasirids may have subsequently lost the elongated foot and mining behaviour by pedomorphosis, which was previously invoked to explain the simple gill structure and small size of many non-symbiotic thyasirids¹⁸. Chemosymbiotic thyasirids, on the other hand, have taken sulphide mining to the extreme, by pushing the limits of hydrostatic extension for the benefit of bacterial symbionts. □

Methods

Thyasirids were collected from the Raunefjord (*T. Parathyasira equalis*, *T. obsoleta*, *T. (Mendicula) ferruginea*) and from Dolviken (*T. flexuosa*, *T. sarsi*), near Bergen, Norway. Sediment collected by Van Veen grab from the Raunefjord site was passed through a 1-mm sieve and distributed into 12 plexiglass aquaria (dimensions: 25 cm × 25 cm × 12 mm; inner width, 6 mm). The aquaria were subdivided into two groups, in which the sediment settled for four days ('low sulphide') or four weeks ('high sulphide') before the introduction of bivalves at the sediment surface. The aquaria were kept in 60-litre tanks containing aerated sea water, replaced daily, and phytoplankton from the Raunefjord (average concentration, 6.4×10^6 cells ml⁻¹). The tanks were maintained in the dark, at 8 °C. After 7, 14 and 21 days, the aquaria were X-rayed (instrument settings: 65 kV, 50 mA). On the X-radiographs, the thyasirids could not always be identified to the species level. However, symbiotic and non-symbiotic thyasirids could be distinguished on the basis of size (the non-symbiotic species were consistently smaller). The day after X-rays were taken, a thin core of sediment was extracted from each aquarium and pore water from each 5-cm interval was isolated by centrifugation. The sulphide content in each fraction was determined using a colorimetric method¹⁹.

Received 24 July; accepted 25 September 2003; doi:10.1038/nature02095.

- Childress, J. J., Felbeck, H. & Somero, G. N. Symbiosis in the deep sea. *Sci. Am.* **256**, 114–120 (1986).
- Le Pennec, M., Beninger, P. G. & Herry, A. Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats. *Comp. Biochem. Physiol. A* **111**, 183–189 (1995).
- Julian, D., Gaill, F., Wood, E., Arp, A. J. & Fisher, C. R. Roots as a site of hydrogen sulfide uptake in the hydrocarbon seep vestimentiferan *Lamellibrachia* sp. *J. Exp. Biol.* **202**, 2245–2257 (1999).

- Giere, O., Conway, N. M., Gastrock, G. & Schmidt, C. 'Regulation' of gutless annelid ecology by endosymbiotic bacteria. *Mar. Ecol. Prog. Ser.* **68**, 287–299 (1991).
- Dando, P. R., Southward, A. J. & Southward, E. C. Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proc. R. Soc. Lond. B* **227**, 227–247 (1986).
- Dando, P. R. & Southward, A. J. Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. *J. Mar. Biol. Assoc. UK* **66**, 915–929 (1986).
- Seilacher, A. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Hist. Biol.* **3**, 289–311 (1990).
- Allen, J. A. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans. R. Soc. Lond. B* **241**, 421–484 (1958).
- Allen, J. A. Function of the foot in the Lucinacea (Eulamellibranchia). *Nature* **171**, 1117–1118 (1953).
- Payne, C. M. & Allen, J. A. The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. *Phil. Trans. R. Soc. Lond. B* **334**, 481–562 (1991).
- Southward, E. C. Gill symbionts in thyasirids and other bivalve molluscs. *J. Mar. Biol. Assoc. UK* **66**, 889–914 (1986).
- Trueman, E. R., Brown, A. C. & Stenton-Dozey, J. Blood flow in a burrowing bivalve at pedal extension and retraction. *J. Moll. Stud.* **52**, 265–266 (1986).
- Arp, A. J., Childress, J. J. & Fisher, C. R. Metabolic and blood gas transport characteristics of the hydrothermal vent bivalve *Calyptogena magnifica*. *Physiol. Zool.* **57**, 648–662 (1984).
- Childress, J. J., Fisher, C. R., Favuzzi, J. A., Arp, A. J. & Oros, D. R. The role of a zinc-based, serum-borne sulphide-binding component in the uptake and transport of dissolved sulphide by the chemoautotrophic symbiont-containing clam *Calyptogena elongata*. *J. Exp. Biol.* **179**, 131–158 (1993).
- Stanley, S. M. Relation of shell form to life habits in the bivalvia (Mollusca). *Geol. Soc. Am. Mem.* **125**, 1–293 (1970).
- Zuschin, M., Mandic, O., Harzhauser, M. & Pervesler, P. Fossil evidence for chemoautotrophic bacterial symbiosis in the thyasirid bivalve *Thyasira michelottii* from the Middle Miocene (Badenium) of Austria. *Hist. Biol.* **15**, 123–134 (2001).
- McAlester, A. L. Evolutionary and systematic implications of a transitional ordovician lucinoid bivalve. *Malacologia* **3**, 433–439 (1966).
- Reid, R. G. B. & Brand, D. G. Sulfide-oxidizing symbiosis in lucinaceans: implications for bivalve evolution. *Veliger* **29**, 3–24 (1986).
- Gilboa-Garber, N. Direct spectrophotometric determination of inorganic sulfide in biological materials and in other complex mixtures. *Anal. Biochem.* **43**, 129–133 (1971).

Acknowledgements We thank J. B. C. Jackson, N. D. Holland and E. Kisfaludy for discussion and advice, and A. Aadnesen, P. Johannessen, T. Sorlie and T. Høisæter for help in collecting thyasirids and running experiments at the University of Bergen Biological Station, Espregrennd. We are grateful to O. K. Dalland and A. Lerheim for allowing the use of X-ray equipment at the veterinary clinic at Stend, Norway. This work was supported by the Scripps Institution of Oceanography graduate department, the Baxter and Alma Ricard Foundation, and the National Science Foundation.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to S.C.D. (sdufour@ucsd.edu).

Governance and the loss of biodiversity

R. J. Smith¹, R. D. J. Muir¹, M. J. Walpole¹, A. Balmford² & N. Leader-Williams¹

¹Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent CT2 7NS, UK

²Conservation Biology Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Most of the world's biodiversity occurs within developing countries that require donor support to build their conservation capacity¹. Unfortunately, some of these countries experience high levels of political corruption², which may limit the success of conservation projects by reducing effective funding levels and distorting priorities³. We investigated whether changes in three well surveyed and widespread components of biodiversity were associated with national governance scores and other socio-economic measures. Here we show that governance scores were correlated with changes in total forest cover, but not with changes in natural forest cover. We found strong associations between governance scores and changes in the numbers of African

elephants and black rhinoceroses, and these socio-economic factors explained observed patterns better than any others. Finally, we show that countries rich in species and identified as containing priority areas for conservation have lower governance scores than other nations. These results stress the need for conservationists to develop and implement policies that reduce the effects of political corruption and, in this regard, we question the universal applicability of an influential approach to conservation that seeks to ban international trade in endangered species.

Political corruption, defined as the unlawful use of public office for private gain², can be an important obstacle to both economic and social development³. Corruption reduces levels of international and national investment, lowers government spending on public services and favours the establishment of projects that allow the misappropriation of funds⁴. This has led to demands by some donor agencies that their future economic assistance to corrupt countries is linked to improved governance and accounting procedures. At the same time, the donor community is being pressed to increase funding to reduce the threat of biodiversity loss and to build conservation capacity¹. The sums needed to conserve biodiversity are small relative to its total economic value^{1,5,6}, but still large in absolute terms⁷. Therefore, current debates centre on ensuring that conservation funds are raised and spent efficiently^{8,9}.

Although evidence from case studies suggests that corruption may affect the outcomes of conservation projects^{10–13}, no study has formally assessed the broader significance of governance to international conservation efforts. This is surprising, because there are several reasons for expecting conservation to be particularly susceptible to subversion by corrupt officials. First, many projects are short term and funded externally, increasing the scope for misappropriation of funds. Second, most government officials are poorly paid, which encourages the acceptance of bribes, and this is particularly likely when they are responsible for managing natural resources with high financial value. Third, conservation departments tend to lack political weight, making it difficult to prevent transgressions by other sectors, such as the armed forces¹³. Finally, measuring the success of conservation projects is difficult¹⁴, allowing corrupt practices to remain hidden. Based on these concerns, we sought to investigate the potential effect of corruption on biodiversity conservation by addressing two key questions. First, are changes in three well surveyed and widespread components of biodiversity—namely forests, African elephants and black rhinoceroses—correlated with governance scores? Second, is there any link between those countries that have been identified as conservation priorities and governance scores?

National governance scores were based on a system that assigns a maximum value of 10 to the least-corrupt countries². Such scores may also be related to a number of other socio-economic factors, and so a preliminary analysis tested for correlations between governance scores and per capita gross domestic product (GDP), Human Development Index (HDI) scores and population density (see Methods). Using Pearson's (r) and Spearman's (r_s) correlations, governance scores were found to be positively correlated with per capita GDP ($n = 75$, $r = 0.847$, $P < 0.001$) and HDI scores ($n = 73$, $r = 0.713$, $P < 0.001$), but not with population density ($n = 77$, $r_s = 0.045$, $P = 0.697$), and all four factors were used in subsequent correlation and stepwise multiple regression analyses.

Our first main analysis investigated links between national governance scores and changes in forest cover. This was because illegal logging is a problem in many countries, and data on forest cover change are available for a large number of nations. Previous studies have related these changes to poverty levels, population density and governance types^{15,16}. Therefore, we tested whether national changes in forest cover between 1990 and 1995 were associated with mean governance scores, as well as mean per capita GDP, mean HDI scores and mean population density (see Sup-

plementary Information). We found that change in total forest cover, which included plantations, was correlated with mean per capita GDP ($n = 101$, $r_s = 0.577$, $P < 0.001$) and mean governance scores ($n = 106$, $r_s = 0.556$, $P < 0.001$; Fig. 1). However, change in natural forest was not correlated with mean governance scores ($n = 83$, $r_s = 0.181$, $P = 0.102$), suggesting that the result for total cover was driven by the establishment of new plantations in wealthier, better-governed countries. This might seem surprising, as corruption has been linked to deforestation¹⁷. However, logging is also used more widely as an economic development policy, which may explain why no pattern was observed.

Corruption might play a larger role when trying to circumvent trade bans underpinned by international law. The African elephant and black rhinoceros are now fully protected by the Convention on International Trade in Endangered Species (CITES), in response to continued demand for ivory and rhinoceros horn. A previous study related population changes in the early 1980s to national spending per km² of protected area (PA)¹⁸. Therefore, we used stepwise multiple regression modelling for which we give both degrees of freedom ($f_{x,y}$) and the regression coefficient (B), to find whether mean governance scores, national spending per km² of PA, mean per capita GDP, mean HDI scores and mean human population densities were related to changes in elephant and rhinoceros numbers between 1987 and 1994^{19,20}, a period when numbers of both species declined (see Supplementary Information). We found that changes in numbers during this period were related only to governance score, for both African elephants ($F_{1,20} = 20.38$, $B = 27.37$, $P < 0.001$, $r^2 = 0.531$; Fig. 2a) and black rhinoceroses ($F_{1,9} = 20.33$, $B = 36.93$, $P = 0.003$, $r^2 = 0.744$; Fig. 2b).

These results suggest that political corruption may play a considerable role in determining the success of national strategies to conserve these two flagship species, despite the international attention they both attract. National spending per km² of PA was not related to population change for either species (African elephants: $P = 0.218$; black rhinoceroses: $P = 0.386$), but this change from the early 1980s probably reflects the development of conservation strategies that focus greater financial resources on protecting key populations, the effectiveness of which is not captured in data on national spending. Such strategies have helped numbers of both species to increase since 1994, but stepwise multiple regression modelling showed that the strength of both recoveries between 1994 and 1998 was again related to mean governance scores alone (African elephants using log₁₀ modelled governance scores:

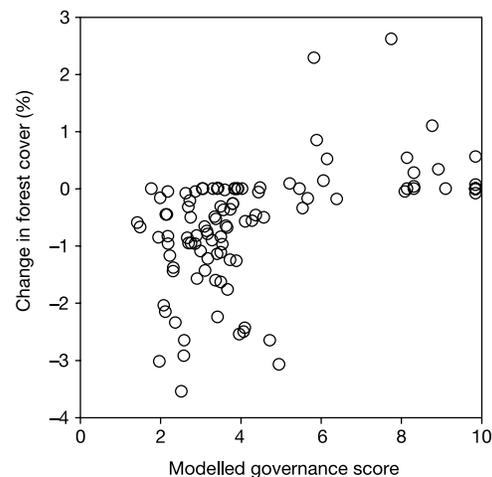


Figure 1 Mean modelled governance scores and changes in total national forest cover, 1990–95.

$F_{1,18} = 7.06$, $B = 181.55$, $P = 0.017$, $r^2 = 0.306$; black rhinoceroses: $F_{1,9} = 19.63$, $B = 32.23$, $P = 0.003$, $r^2 = 0.737$). The model for African elephants during this recovery period predicts that countries with governance scores of less than 3.1 would show population declines. Interestingly, the mean governance score in 2002 for the six Asian elephant range states with available data is 2.9, and total Asian elephant numbers have continued to decline, despite the CITES ban on trade in ivory.

As results suggest that corruption may affect the success of conservation efforts, we also investigated corruption levels in countries identified as global priorities for conservation funding (see Supplementary Information). There is indeed a negative relationship between governance scores and combined bird and mammal species richness, adjusted for country area ($n = 83$, $r_s = -0.473$, $P < 0.001$; Fig. 3). However, most non-governmental organizations (NGOs) that donate funds for conservation do not set their national priorities on species richness alone. Therefore, we investigated the governance scores of countries that contain priority areas identified by three NGOs, based on endemism, threat and representativeness. We found that countries containing Endemic Bird Areas²¹ (EBAs), biodiversity hotspots²² and Focal 25 terrestrial ecoregions²³ all had lower governance scores than those countries that did not (Table 1).

These results highlight the need for the conservation community to develop approaches that offset the effects of poor governance.

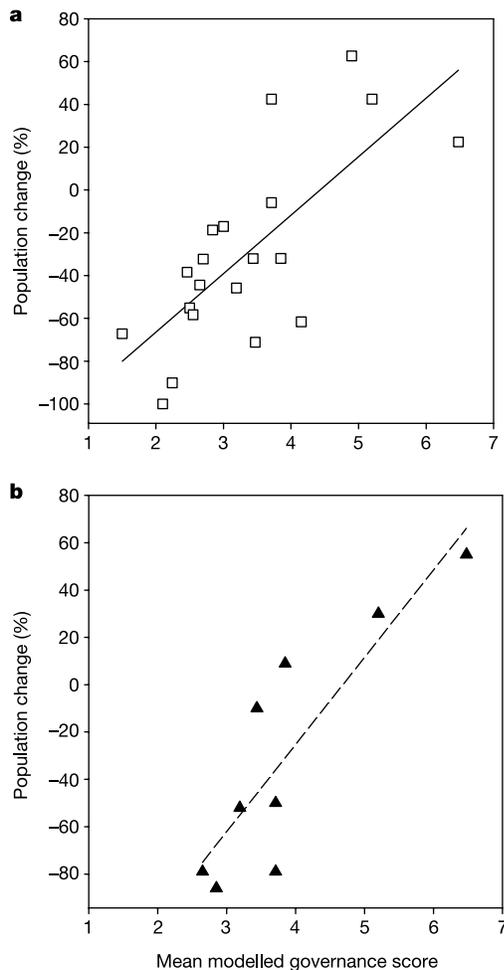


Figure 2 Mean modelled governance scores and changes in national populations of two species, 1987–94. **a**, African elephants; **b**, black rhinoceroses.

Table 1 Governance scores and priority areas for conservation

Priority area type	Mean governance scores		t statistic
	Contains	Outside	
BirdLife EBAs	3.65	6.37	5.61*
CI hotspots	3.86	5.86	3.90*
WWF Focal 25	3.31	5.42	4.62*

EBA, Endemic Bird Area; CI, Conservation International; WWF, WorldWide Fund for Nature. * $P < 0.001$

They also support the ample anecdotal evidence that links corruption and conservation failure both within PAs, where staff can be bribed to allow transgressions, and outside PAs, where communities lack the capacity to protect natural resources from corrupt officials²⁴. Simplistically, our results might suggest focusing donor investment on better governed countries. However, this would be unwise, as many countries with poor governance have high levels of species endemism, as well as distinctive populations of widespread species, and should not be neglected. Instead, successful conservation projects in poorly governed countries show that these problems can be reduced by developing a motivated, well paid workforce²⁵, using more stringent accounting procedures and engaging the private sector in management partnerships²⁶.

The international donor community should, therefore, continue to use their influence to encourage appropriate reforms²⁷. They should also publicly differentiate between genuine conservation priorities and crisis events caused by poor governance, avoiding the temptation to use the latter as fund-raising opportunities or reasons for changing international policies. However, there is also a need for a broad review of present conservation practice to develop systems that are less open to subversion. For example, outlawing international trade in endangered species continues to be championed as a universally applicable approach to conservation. This is despite evidence that these bans are ineffective in poorly governed countries if demand remains high, and that they encourage bribery and increase the power of corrupt officials²⁸. At present, any policy review is hampered by a lack of relevant data and an unwillingness to discuss project-based issues associated with corruption. Instead, the conservation community needs to accept that these problems must be identified and discussed openly if they are to be resolved. □

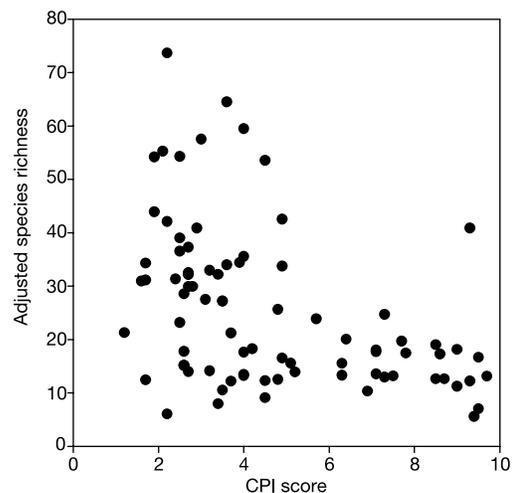


Figure 3 National governance scores and adjusted species richness.

Methods

The governance scores were based on the Corruption Perception Index (CPI) produced by Transparency International². This system uses independent surveys of business people and assessments by country analysts to compare national corruption levels. However, it was only initiated in 1995, so another data set, the International Country Risk Guide (ICRG), was used to provide information for earlier years. The ICRG system uses several coarse-scale factors to measure national governance levels, and a data set was available that contained information on 126 countries between 1984 and 1999. Therefore, we used stepwise linear regression analysis to produce a model that allowed \log_{10} CPI scores to be calculated on the basis of these ICRG data. This model was developed using data for 1999 and included three ICRG factors, which were 'corruption' ($B = 0.074$, $P < 0.001$), 'bureaucratic quality' ($B = 0.0057$, $P < 0.001$) and 'law and order' ($B = 0.0028$, $P = 0.008$). In this system, 'corruption' measures corruption within the political system, 'bureaucratic quality' measures the ability of the bureaucracy to govern without drastic changes in policy or implementation, and 'law and order' measures both popular observance of the law and the strength and impartiality of the legal system. The model explained most of the observed variation ($F_{3,91} = 122.68$, adjusted $r^2 = 0.809$) and comparisons of predicted and actual CPI scores for 1995 and 1996 showed that the model had high levels of explanatory power, which were increased in the latter period when data on a more representative number of developing countries were available (1995: $n = 40$, $r^2 = 0.728$; 1996: $n = 53$, $r^2 = 0.860$). Therefore, we used this model to calculate CPI scores for those analyses that used biodiversity data collected before 1995.

Data obtained by the Food and Agriculture Organization on changes in forest cover between 1990 and 1995, together with information on African elephant populations¹⁹ and black rhinoceros populations²⁰ were collated as the best available data on changes in widespread biodiversity elements. We also collated data on annual per capita Gross Domestic Product (GDP), Human Development Index (HDI) scores produced by the United Nations Development Programme and human population density data. Data on national conservation budgets were available from one of a range of years from 1991 to 1996 for a number of African countries²⁹, so these were adjusted to 1993 US\$ (the median date) using deflation indexes produced by the International Monetary Fund. Spearman's rank correlation tests and stepwise multiple regression modelling were then used to identify factors that were related to national percentage change in these biodiversity components. These factors were transformed, whenever necessary, to meet the assumptions of the tests. In each case, data from countries with a restricted amount of each component were excluded, as small changes or measurement errors were more likely to produce apparently extreme results. The exclusion levels were: forest area $< 30,000 \text{ km}^2$, elephant populations $< 1,000$ and black rhinoceros populations < 10 .

We used CPI scores for 2002 to investigate the relationships between national biodiversity levels and governance. Species richness values for each country were calculated as the number of recorded mammal and bird species, using data available from the World Resource Institute. We corrected for the nonlinear relationship between species number and country area by dividing species number by A^z , where A is country area, and z is a typical value for the slope of a nested, within-continent plot of $\log(\text{species number})$ on $\log(\text{area})$, set here as 0.25 (ref. 30).

Received 6 June; accepted 22 August 2003; doi:10.1038/nature02025.

- Balmford, A. *et al.* Ecology—Economic reasons for conserving wild nature. *Science* **297**, 950–953 (2002).
- Transparency International *Corruption Perceptions Index 2002* (Transparency International, Berlin, 2002).
- Kaufmann, D. Corruption: The facts. *Foreign Policy* **107**, 114–131 (1997).
- Azfar, O., Lee, Y. & Swamy, A. The causes and consequences of corruption. *Ann. Am. Acad. Polit. Sci.* **573**, 42–56 (2001).
- Costanza, R. *et al.* The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260 (1997).
- Balmford, A., Gaston, K. J., Blyth, S., James, A. & Kapos, V. Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc. Natl Acad. Sci. USA* **100**, 1046–1050 (2003).
- James, A., Gaston, K. J. & Balmford, A. Can we afford to conserve biodiversity? *Bioscience* **51**, 43–52 (2001).
- Hughey, K. F. D., Cullen, R. & Moran, E. Integrating economics into priority setting and evaluation in conservation management. *Conserv. Biol.* **17**, 93–103 (2003).
- Balmford, A. & Whitten, T. Who should pay for tropical conservation, and how could the costs be met? *Oryx* **37**, 238–250 (2003).
- Barnes, R. F. W., Blom, A. & Alers, M. P. T. A review of the status of forest elephants *Loxodonta africana* in Central Africa. *Biol. Conserv.* **71**, 125–132 (1995).
- Archabal, K. & Naughton-Treves, L. Tourism revenue-sharing around national parks in Western Uganda: Early efforts to identify and reward local communities. *Environ. Conserv.* **28**, 135–149 (2001).
- Myers, N. *The Primary Source: Tropical Forests and our Future* (Norton & Co, New York, 1992).
- Robertson, J. M. Y. & van Schaik, C. P. Causal factors underlying the dramatic decline of the Sumatran orang-utan. *Oryx* **35**, 26–38 (2001).
- Salafsky, N., Margoluis, R., Redford, K. H. & Robinson, J. G. Improving the practice of conservation: A conceptual framework and research agenda for conservation science. *Conserv. Biol.* **16**, 1469–1479 (2002).
- Didia, D. O. Democracy, political instability and tropical deforestation. *Glob. Environ. Change* **7**, 63–76 (1997).
- Geist, H. J. & Lambin, E. F. Proximate causes and underlying driving forces of tropical deforestation. *Bioscience* **52**, 143–150 (2002).
- Jepson, P., Jarvie, J. K., MacKinnon, K. & Monk, K. A. The end for Indonesia's lowland forests? *Science* **292**, 859 (2001).
- Leader-Williams, N. & Albon, S. D. Allocation of resources for conservation. *Nature* **336**, 533–535 (1988).

- Barnes, R. F. W. *et al.* *African Elephant Database 1998* (IUCN/SSC African Elephant Specialist Group, IUCN, Gland, Switzerland, 1999).
- Emslie, R. & Brooks, M. *African Rhino: Status Survey and Conservation Action Plan* (IUCN/SSC African Rhino Specialist Group, IUCN, Gland, Switzerland, 1999).
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation* (BirdLife International, Cambridge, UK, 1998).
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- World Wide Fund For Nature *Living Planet Campaign: A Call to Action* (WWF, Washington DC, 1999).
- Whitten, T., Holmes, D. & MacKinnon, K. Conservation biology: A displacement behavior for academia? *Conserv. Biol.* **15**, 1–3 (2001).
- Leakey, R. & Morell, V. *Wildlife Wars: My Battle to Save Kenya's Elephants* (Pan Macmillan, London, 2001).
- Walpole, M. J. & Leader-Williams, N. Masai Mara tourism reveals partnership benefits. *Nature* **413**, 771 (2001).
- International Institute for Environment and Development *Whose Eden? An Overview of Community Approaches to Wildlife Management* (IIED, London, 1994).
- Oldfield, S. *The Trade in Wildlife: Regulation for Conservation* (Earthscan, London, 2002).
- James, A., Green, M. J. B. & Paine, J. R. (eds) *A Global Review of Protected Area Budgets and Staff* (WCMC-World Conservation Press, Cambridge, UK, 1999).
- Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, UK, 1995).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank the Durrell Institute for Conservation and Ecology for providing funding, and K. Brandon, N. Burgess, S. Elton, R. Green, J. Groombridge, A. Huggins, S. Thornton and T. Whitten for advice.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to R.J.S. (R.J.Smith@kent.ac.uk).

Sophisticated sperm allocation in male fowl

Tommaso Pizzari^{1*}, Charles K. Cornwallis², Hanne Løvlie³, Sven Jakobsson³ & Tim R. Birkhead²

¹Department of Animal Environment & Health, Swedish University of Agricultural Sciences, Skara PO Box 234, SE-532 23, Sweden

²Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

³Department of Zoology, Stockholm University, Stockholm SE-106 91, Sweden

* Present address: School of Biology, The University of Leeds, Leeds LS2 9JT, UK

When a female is sexually promiscuous, the ejaculates of different males compete for the fertilization of her eggs¹; the more sperm a male inseminates into a female, the more likely he is to fertilize her eggs². Because sperm production is limited and costly, theory predicts that males will strategically allocate sperm (1) according to female promiscuity^{1,3–5}, (2) saving some for copulations with new females^{3,6,7}, and (3) to females producing more and/or better offspring^{3,8}. Whether males allocate sperm in all of these ways is not known, particularly in birds where the collection of natural ejaculates only recently became possible. Here we demonstrate male sperm allocation of unprecedented sophistication in the fowl *Gallus gallus*. Males show status-dependent sperm investment in females according to the level of female promiscuity; they progressively reduce sperm investment in a particular female but, on encountering a new female, instantaneously increase their sperm investment; and they preferentially allocate sperm to females with large sexual ornaments signalling superior maternal investment. Our results indicate that female promiscuity leads to the evolution of sophisticated male sexual behaviour.

In the fowl, socially dominant males have privileged copulatory