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 haemocoel. 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 heart), 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. Transport of sulphide from the foot to the gills has previously been proposed for the chemosymbiotic bivalves *Calyptogena magnifica* and *Calyptogena elongata*.

The sulphide mining behaviour could have been derived from the use of the foot in anterior inhalant tube formation, characteristic of Lucinaceae (lucinids, thyasirids and ungulinids). On X-radiographs of the non-chemosymbiotic ungulid *Diplodonta notata*, some burrows are directed towards the sediment surface, whereas others lead deeper into the sediment, apparently having been misdirected. 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 under-neath measuring 15 times the shell length, has been discovered in Lower Austria. The burrowing behaviour of thyasirids seems to have appeared early in the evolution of the family, whose fossil record goes back to the Cretaceous period. 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 paedomorphosis, which was previously invoked to explain the simple gill structure and small size of many non-symbiotic thyasirids. 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. (Parathyasia) equulis*, *T. eboluta*, *T. (Mendicula) verruginea*) and from Dolviken (*T. flexuosa*, *T. sarvi*), 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 cm; 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 × 10⁴ 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 shell 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 method.

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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 gain, can be an important obstacle to both economic and social development. 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 funds. 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 capacity. The sums needed to conserve biodiversity are small relative to its total economic value, but still large in absolute terms. Therefore, current debates centre on ensuring that conservation funds are raised and spent efficiently.

Although evidence from case studies suggests that corruption may affect the outcomes of conservation projects, 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 forces. Finally, measuring the success of conservation projects is difficult, 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 countries. 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 (rs) 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, rs = 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. 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 Supplementary Information). We found that change in total forest cover, which included plantations, was correlated with mean per capita GDP (n = 101, rs = 0.577, P < 0.001) and mean governance scores (n = 106, rs = 0.556, P < 0.001; Fig. 1). However, change in natural forest was not correlated with mean governance scores (n = 83, rs = 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 deforestation. 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). Therefore, we used stepwise multiple regression modelling for which we give both degrees of freedom (F, s) 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, 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 (F₁,₂₀ = 20.38, B = 27.37, P < 0.001, r² = 0.531; Fig. 2a) and black rhinoceroses (F₁,₉ = 20.33, B = 36.93, P = 0.003, r² = 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: 0.003; Fig. 2b).

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 Areas (EBAs), biodiversity hotspots and Focal 25 terrestrial ecoregions 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.

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 officials. 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 workforce, using more stringent accounting procedures and engaging the private sector in management partnerships.

The international donor community should, therefore, continue to use their influence to encourage appropriate reforms. 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 officials. 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.

### Table 1 Governance scores and priority areas for conservation

<table>
<thead>
<tr>
<th>Priority area type</th>
<th>Mean governance scores</th>
<th>t statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Contains</td>
<td>Outside</td>
<td></td>
</tr>
<tr>
<td>BirdLife EBAs</td>
<td>3.65</td>
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</tr>
<tr>
<td>CI hotspots</td>
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</tr>
<tr>
<td>WWF Focal 25</td>
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* $P < 0.001$

![Figure 2](image2.png) **Figure 2** Mean modelled governance scores and changes in national populations of two species, 1987–94. a, African elephants; b, black rhinoceroses.

![Figure 3](image3.png) **Figure 3** National governance scores and adjusted species richness.
When a female is sexually promiscuous, the ejaculates of different males compete for the fertilization of her eggs; the more sperm a male inseminates into a female, the more likely he is to fertilize her eggs. 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 sperm for copulations with new females (3,6,7), and (3) to females producing a higher number of offspring (1). Male sperm allocation is a balance between fertility and sperm competition, and it is influenced by various factors such as female promiscuity, sperm competition, and the number of sperm stored.

**Sophisticated sperm allocation in male fowl**

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