

transgressive phase of lake sedimentation and most closely associated with the equally minute, and equally abundant, acanthodian *Mesacanthus*. It seems likely that they were transported from a sheltered shallow-water environment and deposited *post mortem* in relatively deep water. The exceptional preservation of internal skeletal details might be associated with the absence of squamation¹³. In associated *Mesacanthus* of the same size, the dermal scale covering is complete, making a casing inside which the internal structures would have rotted very quickly before burial.

Dipterus valenciennesi is the only lungfish in the Achanarras fauna and the single most abundant taxon. Therefore, although there are no characters on which a formal synonymy could be based, economy of hypothesis suggests that it is the adult form of *Palaeospondylus gunni*. Evidently this lungfish spent its whole life cycle in fresh water; the early stages involved a separate naked, sessile stage during which it lived off the contents of the yolk-sac and used its attachment organ to attach to vegetation or the substrate. The local abundance and patchy vertical distribution of the larva suggests that the environments in which it lived, before being swept into the deeper water and deposited, were strongly seasonal in occurrence and of limited geographic distribution, such as seasonally flooded, sheltered bays or marshes where the fry of *Mesacanthus* and the larvae of lungfishes could survive. □

Methods

Serial sections were reconstructed to three dimensions by the assembly of images into volume models, the calculation of isosurfaces and the visualization of the resulting surfaces by ray-tracing¹⁴. Images underwent manual 'virtual preparation' before visualization to ensure that the true edge of the fossil was modelled and to apply false colour to discrete structures¹⁵.

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Impact of localized badger culling on tuberculosis incidence in British cattle

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Pathogens that are transmitted between wildlife, livestock and humans present major challenges for the protection of human and animal health, the economic sustainability of agriculture, and the conservation of wildlife. *Mycobacterium bovis*, the aetiological agent of bovine tuberculosis (TB), is one such pathogen. The incidence of TB in cattle has increased substantially in parts of Great Britain in the past two decades, adversely affecting the livelihoods of cattle farmers and potentially increasing the risks of human exposure. The control of bovine TB in Great Britain is complicated by the involvement of wildlife, particularly badgers (*Meles meles*), which appear to sustain endemic infection and can transmit TB to cattle¹. Between 1975 and 1997 over 20,000 badgers were culled as part of British TB control policy, generating conflict between conservation and farming interest groups². Here we present results from a large-scale field trial^{3–5} that indicate that localized badger culling not only fails to control but also seems to increase TB incidence in cattle.

Bovine TB is primarily a disease of cattle but it can be transmitted to people. A 1934 inquiry reported that 40% of dairy cattle in the United Kingdom were infected⁶, with bovine TB causing about 2,000 human deaths annually (6% of the total deaths from TB at that time)⁷. The risk of human infection has been reduced greatly since then, both by pasteurization of milk and by regular tuberculin testing of cattle, with compulsory slaughter of animals showing evidence of exposure. Several countries have effectively controlled TB by this approach, but control has been more difficult to achieve where wildlife act as reservoir hosts that continually re-infect cattle populations. In the British Isles badgers are strongly implicated in transmitting TB to cattle, and badger culling has formed a component of British TB control policy since 1973 (refs 1, 2).

Badger culling strategies have been modified several times^{1,2} (Fig. 1). Badgers were first linked to cattle TB in 1973 and farmers were licensed to cull them. From 1975 to 1981 badgers were gassed in their setts using hydrogen cyanide. This was replaced by the 'clean ring' strategy, designed to identify and remove clusters of infected badgers. From 1986 to 1998 culling occurred only on land used by tuberculin-positive cattle. This was intended as an 'interim strategy' pending development of a more selective culling policy⁸. The effectiveness of these strategies at controlling cattle TB remained unknown because they were not compared with one another, or with a strategy of no culling, in a rigorous randomized trial. The Independent Scientific Group on Cattle TB designed and is overseeing a large-scale trial aimed at evaluating two options of badger

Table 1 History of badger culling in trial areas

Triplet	Treatment	First reactive cull	Badgers culled in reactive treatment	First interim cull	Last interim cull	Years of interim culling	Badgers culled under interim strategy
A	Reactive	2000	117	1992	1997	6	300
	No culling	–	–	1988	1998	7	186
B	Reactive	1999	301	1987	1998	10	314
	No culling	–	–	1987	1997	10	342
C	Reactive	2000	394	1988	1998	7	168
	No culling	–	–	1992	1997	6	319
D	Reactive	2003	122	1995	1997	3	64
	No culling	–	–	1997	1997	1	14
E	Reactive	2002	169	1986	1997	12	455
	No culling	–	–	1986	1998	10	239
F	Reactive	2002	435	1986	1997	10	357
	No culling	–	–	1989	1998	9	240
G	Reactive	2002	256	–	–	0	0
	No culling	–	–	–	–	0	0
H	Reactive	2002	159	1993	1998	5	126
	No culling	–	–	1992	1997	5	31
I	Reactive	2003	94	1997	1998	2	35
	No culling	–	–	1994	1998	5	38
J	Reactive	–	0	1996	1997	2	94
	No culling	–	–	–	–	0	0

The data include reactive culling (in the course of this study) and culling under the interim strategy that preceded this study (1986–98). The fourth column gives the number of badgers culled up to 17 September 2003; the seventh column refers to the number of calendar years in which at least one interim cull occurred.

culling as a means to reduce TB incidence in cattle^{1–5}.

The trial commenced in 1998 and has involved three experimental treatments: (1) localized reactive culling, which seeks to remove badgers from small areas in response to TB outbreaks in cattle; (2) proactive culling, which aims to reduce badger densities to low levels across entire trial areas; and (3) no culling. Of these treatments reactive culling was most similar to past policies, in that it used cattle TB outbreaks as a sentinel for the presence of potentially infectious badgers, whose removal might be expected to reduce the risk of future outbreaks. All aspects of the trial design have been published^{3–5}, and many have been subjected to independent audit^{9–12}. Regular field surveys have indicated changes in badger activity consistent with the aims of the culling treatments; badger activity was lowest in areas subjected to proactive culling, and highest in no culling areas¹³. Trial areas varied in the extent to which they had experienced badger culling in the past (Table 1).

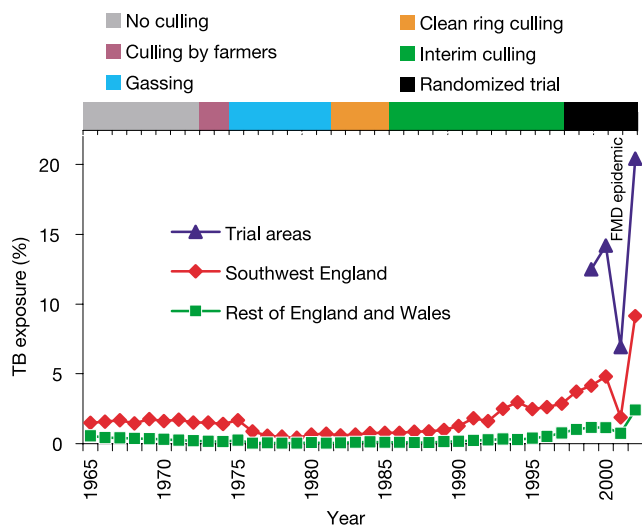


Figure 1 Percentage of total cattle herds found to show evidence of exposure to TB (in confirmed and unconfirmed breakdowns) based on routine testing, and the badger culling policies in operation at the time. Incidence was higher in trial areas because they were placed in areas of highest risk; however, the herds in trial areas experienced temporal trends in TB incidence similar to those throughout England and Wales. Most tests scheduled to occur during the foot-and-mouth disease (FMD) epidemic were delayed until 2002, hence incidence seems low in 2001 and high in 2002.

We compared TB incidence rates (up to 31 August 2003) in cattle herds subjected to the different treatments using log-linear Poisson regression for the number of confirmed breakdowns recorded in each trial area since enrolment. A confirmed herd breakdown is an occasion on which at least one member of a cattle herd showed evidence of TB exposure that was subsequently confirmed by culture of *M. bovis* or by identification of visible lesions of TB at post-mortem examination. In the absence of such confirmation, the breakdown is ‘unconfirmed’. A herd breakdown is also confirmed when suspect TB lesions are found in carcasses of animals during routine slaughterhouse meat inspection and those lesions yield *M. bovis* on bacteriological culture. The results presented here concern the effect of reactive culling only.

Our analysis revealed that the reactive treatment has thus far been associated with a 27% increase in the incidence of cattle herd breakdowns ($P = 0.0145$; standard 95% confidence interval of 4.8–53% increase) when compared with no culling areas. This result was highly consistent, with more breakdowns than expected in all nine of the reactively culled areas (Fig. 2). Triplet J had not yet received any reactive culling (Table 1). After adjustment for covariates (see Methods) there was relatively little extra-Poisson variation. The inflation factor (the square root of the model deviance divided by the degrees of freedom) was equal to 1.37 with the goodness-of-

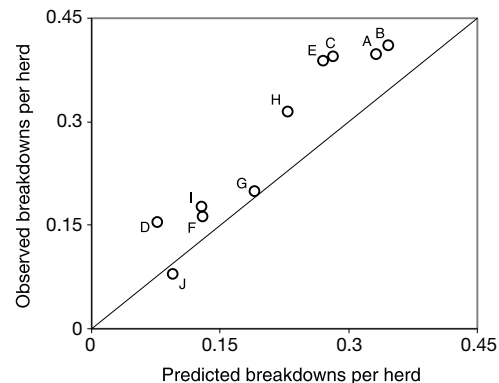


Figure 2 Triplet-specific TB incidence in reactive trial areas (the number of confirmed breakdowns since enrolment in the trial, on completion of the initial proactive cull, divided by the number of baseline herds at risk) observed and predicted had these areas received no culling. Points above the line indicate that increased incidence occurred in reactively culled trial areas. Points have differing precisions and no reactive culling had been carried out in triplet J by September 2003.

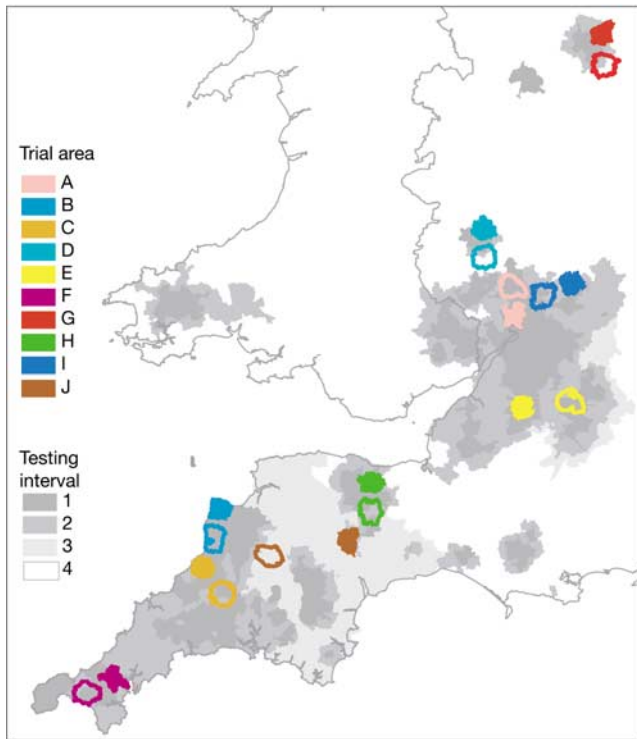


Figure 3 Map of reactive (filled shapes) and no culling (outlined shapes) trial areas superimposed over the 1998 testing intervals for cattle (1-yr testing is conducted in areas of highest incidence, 4-yr testing in areas of lowest incidence). All herds in trial areas have been subjected to annual testing throughout the trial.

fit *P*-value equal to 0.02. However, even if the confidence interval were conservatively expanded using this factor, the resulting interval—2.4% decrease to 65% increase—does not change the conclusion that localized reactive culling is highly unlikely to decrease substantially TB incidence in cattle.

On the basis of these findings we conclude that reactive culling of badgers, as carried out in the trial, is unlikely to contribute to the control of cattle TB. Our original trial design called for at least one complete year of enrolment in all trial areas (which would occur in late December 2003)⁴; however, as our results show that reactive culling is unlikely to offer a viable base for future policy, we support the decision to discontinue it as an experimental treatment. We recommend, however, that the proactive and no culling treatments be continued until the estimate of any effect is sufficiently precise to inform policy.

Our finding of a consistent increase in cattle TB incidence in response to reactive badger culling provides evidence for a link between badgers and TB in cattle, but points to transmission dynamics that must be highly complex. Control is known to disrupt badger social organization, prompting long-distance movement and dispersal^{14–16}. Such movements are associated with increased TB transmission among badgers¹⁷, and may also influence infection risk for cattle. Studies are underway to investigate this issue.

Our findings may also influence the interpretation of experiments carried out in the Republic of Ireland, where badger culling has been linked with substantial reductions in the incidence of cattle TB¹⁸. Past¹⁸ and ongoing¹⁹ studies compare the incidence of cattle TB in ‘project’ areas subject to intensive, widespread proactive culling of badgers, with that in ‘reference’ areas where badgers are culled only in response to TB outbreaks in cattle. As our study demonstrates that reactive culling is associated with an increased incidence of cattle TB relative to no culling, the Irish studies (which lack no-culling experimental control areas) may over-estimate the true effectiveness of widespread proactive culling.

The reactive culling treatment was similar to badger culling policies operating nationwide in Great Britain before the start of the trial. Hence, it is possible that these past approaches may have been similarly ineffective. During the operation of the ‘interim’ culling strategy, the herd incidence of cattle TB in southwest Britain rose from 0.75% in 1986 to 2.61% in 1996 (ref. 1). Although it is unlikely that this historic increase was entirely attributable to the badger culling policy (Northern Ireland experienced a similar increase in the absence of badger culling²⁰), our results suggest that this form of culling may have been of no benefit to the control of TB in British cattle. □

Methods

Trial design

Thirty trial areas, each covering approximately 100 km², were selected in areas of highest TB risk to cattle (Fig. 3), and were recruited sequentially as ten matched ‘triplets’. All trial areas were surveyed for signs of badger activity, and then randomly assigned to treatments in such a way that each treatment was replicated ten times, once within each triplet. Immediately after randomization, an initial proactive cull was carried out in the appropriate area of each triplet. The first such cull was completed in November 1998 and the tenth and final cull in December 2002. Once the initial proactive cull was complete, data on cattle TB incidence in all three trial areas in the triplet were collected, and breakdowns that occurred in reactive areas triggered reactive culling. Reactive culls commenced in nine of the ten triplets thereafter (Table 1). Between March and December 2001 during an outbreak of foot-and-mouth disease (FMD) in Great Britain cattle testing was substantially reduced. Badger culling was suspended at the same time, and recommenced in May 2002.

Reactive culling sought to identify and remove all badgers using the same land as cattle herds that had experienced recent TB outbreaks. Survey data on the distribution of badger dens (setts) and other field signs were used to map approximate home ranges; this method⁸ has been shown to provide a good estimate of the disposition of badger territories when based on good survey data^{10,21}. Culling then took place at all active badger setts falling within home ranges that overlapped the land used by the cattle herd that had shown confirmed evidence of TB exposure. Where the spatial organization of badgers could not be discerned, culling took place at all setts within 1 km of the breakdown farm. When breakdowns occurred on more than one farm in an area, a single culling operation could cover multiple breakdowns. The average area covered by reactive culls (5.3 km²) was intermediate between the extent of historic interim (approx 1 km²) and clean ring (approximately 9 km²) operations¹.

Badgers were captured in cage traps, which were placed primarily at badger setts and baited with peanuts. Badgers were despatched by gunshot, a method deemed ‘humane’ by independent audit^{11,12}. Animals other than badgers were released. All badger carcasses were subjected to full post-mortem examination. No culling took place between 1 February and 30 April each year to avoid killing mothers with unweaned cubs.

Statistical analysis

Data on TB incidence in cattle were analysed by log-linear Poisson regression. The regression model adjusted for triplet, the log of the number of baseline herds at risk, and the log of the number of historic confirmed breakdowns. The historic incidence was calculated for the 3-yr period before the initial cull in the proactive area, except in triplets D, I and J where it was calculated for the 3-yr period before the start of the FMD epidemic.

We tested for covariate interactions with treatment effects for: (1) log of the number of baseline herds at risk; (2) log of the number of historic confirmed breakdowns; (3) per cent of occupiers that agreed to culling; (4) log of the number of active main setts; (5) log of the number of badgers culled during the interim strategy; (6) log of the number of badgers taken in initial and first follow-up proactive culls; (7) TB prevalence in badgers culled in the initial proactive culls; and (8) time since enrolment in the trial. None of these were found to be significant. Thus, there was no evidence that reactive culling performed differently in particular settings.

Furthermore, we analysed alternative response variables for different time periods (pre-FMD, post-FMD and from the end of the first follow-up cull in the proactive area) and for the overall number of breakdowns (including both confirmed and unconfirmed). Models were also fitted replacing the log of the number of baseline herds at risk with either the log of the estimated number of cattle at baseline, the log of the number of tests conducted, or the log of the estimated number of cattle tested. The results obtained were similar in each case.

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Authors' contributions J.B., C.A.D., D.R.C., G.G., J.P.M., W.L.M. and R.W. constitute the Independent Scientific Group on Cattle TB, and were jointly responsible for designing and overseeing the study. Statistical analyses were carried out by D.R.C., C.A.D. and A.M.L.F. C.A.D. and R.W. drafted the manuscript, although all authors contributed to its preparation.

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Predicting distributions of known and unknown reptile species in Madagascar

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Despite the importance of tropical biodiversity¹, informative species distributional data are seldom available for biogeographical study or setting conservation priorities^{2,3}. Modelling ecological niche distributions of species offers a potential solution^{4–7}; however, the utility of old locality data from museums, and

of more recent remotely sensed satellite data, remains poorly explored, especially for rapidly changing tropical landscapes. Using 29 modern data sets of environmental land coverage and 621 chameleon occurrence localities from Madagascar (historical and recent), here we demonstrate a significant ability of our niche models in predicting species distribution. At 11 recently inventoried sites, highest predictive success (85.1%) was obtained for models based only on modern occurrence data (74.7% and 82.8% predictive success, respectively, for pre-1978 and all data combined). Notably, these models also identified three intersecting areas of over-prediction that recently yielded seven chameleon species new to science. We conclude that ecological niche modelling using recent locality records and readily available environmental coverage data provides informative biogeographical data for poorly known tropical landscapes, and offers innovative potential for the discovery of unknown distributional areas and unknown species.

The biota of Madagascar represents a global priority for conservation owing to the island's exceptional endemic diversity and ongoing loss of natural habitats¹. However, although substantial expansion of the national protected area network is anticipated⁸, current rates of deforestation are rapidly reducing the country's future conservation options^{9–11}; in some regions, urgent management decisions will have to be made before detailed biological survey data become available. As a result, the ability to predict biodiversity distribution in poorly known regions of the island offers enormous potential for conservation planning. Using an evolutionary computing approach, we present predictive distribution results for 11 chameleon species, in the first application of satellite imagery to ecological distributional modelling for Madagascar.

For an initial test, with 29 environmental GIS (Geographic Information System) base layers of land cover, climate, topography and hydrology, we used random partitions of our recent post-1988 occurrence localities for building and testing ecological niche models for 11 chameleon species. Using 50% of the post-1988 occurrences to predict the remainder of the post-1988 data, this test yielded impressive results: predictions were significantly better than random for all 11 species under the 'all models predict' criteria and for 9 of the 11 species under the 'any model predicts' criteria, with an overall correct prediction success of 62.8% and 83.0% respectively (Table 1).

A second set of tests included pre-1978 localities^{12,13} for testing models. Models based on the same random 50% of the post-1988 occurrences as described above (for predicting post-1988) were used to predict pre-1978 occurrences. These tests produced significant results for fewer species: 4 and 5 of the 9 species, and overall prediction success was reduced to 33.1% and 63.8% (all models predict and any model predicts criteria, respectively), the reduced prediction ability probably reflecting changes in land use across Madagascar, where recent landscape data (used for modelling) less accurately reflect landscape conditions at the historical time of collecting. To investigate the influence of data density, we repeated this test with models based on 100% of the post-1988 data, and overall results were quite similar or slightly improved (models significant for 3 and 6 of the 9 species, 39.2% and 78.5% overall prediction success under the all models predict and any model predicts assumptions, *respectively). The final temporal partition examined the utility of pre-1978 occurrence data to predict post-1988 distributions, in spite of overall low sample sizes for model building. Predictions resulted in significantly better than random for 6 and 8 of the 9 species, although overall correct prediction success was lower than the other tests (28.0% and 57.1% under the all models predict and any model predicts criteria, respectively).

A third set of tests used data from pre-1978, post-1988 and both temporal partitions combined, for building ecological niche models that were then tested with a completely independent test data set,

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