us one step closer to understanding the ecological and evolutionary significance of *Pachysoma's* unusual gait.

Supplemental Information
Supplemental Information including experimental procedures and a movie can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.09.031.

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Badger social networks correlate with tuberculosis infection

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Although disease hosts are classically assumed to interact randomly [1], infection is likely to spread across structured and dynamic contact networks [2]. We used social network analyses to investigate contact patterns of group-living European badgers, *Meles meles*, which are an important wildlife reservoir of bovine tuberculosis (TB). We found that TB test-positive badgers were socially isolated from their own groups but were more important for flow, potentially of infection, between social groups. The distinctive social position of infected badgers may help explain how social stability mitigates, and social perturbation increases, the spread of infection in badgers.

Tuberculosis, caused by *Mycobacterium bovis*, is a zoonotic infection of cattle and is a global challenge in animal health. In the U.S.A., New Zealand, Spain, France, Ireland and Britain, TB control in cattle is complicated by reservoirs of infection in wildlife. In Britain, badgers are a major wildlife reservoir and although intensive, pro-active badger culling can reduce TB incidence in cattle in culled areas, it has also been associated with increases in prevalence in badgers and increases in incidence in cattle in adjacent areas [3,4]. Hence, reductions in badger density appear not to yield quantitatively equivalent reductions in TB transmission. Across much of the species' range, badgers live in territorial social groups that share dens, known as setts, and increases in TB transmission associated with culling have been hypothesised to arise from perturbation of these social structures [5]. Therefore, understanding badger social behaviour and its relationship to infection will help in developing effective TB control strategies.

We used proximity-logging radio tags to monitor patterns of sett use and to record remotely interactions among badgers in an intensively-studied, undisturbed, high-density population at Woodchester Park, Gloucestershire, England. We sampled eight social groups and tagged 51 adult and sub-adult badgers. 21 badgers (41%) tested positive on at least one occasion to at least one of two live-animal diagnostic tests for TB infection. We analysed within-group and among-group contacts separately and derived three measures of social network centrality: Degree (frequency and/or duration of immediate contacts of an individual), Closeness (distance of an individual to all others) and Flow-Betweenness (a measure of positional advantage in the 'flow', potentially of infection, across the network, specifically, the contribution of a given individual to all possible pathways connecting all pairs in the network).

We found statistically significant relationships between network position and TB test outcome (Figure 1). Within-group degree and closeness were lower for test-positive (TB+) than for test-negative (TB–) badgers in autumn and winter, but did not differ significantly in spring and summer; among-group degree and closeness did not differ significantly with respect to infection (see Table S1 in the Supplemental Information). Within-group flow-betweenness was significantly lower for TB+ badgers in autumn, whereas among-group flow-betweenness was significantly higher for TB+ badgers in summer and winter (Table S2). Social behaviour was related to spatial behaviour; time spent resting at outlying setts was negatively related to time spent with badgers from their own group but positively related to time spent with members of other social groups (Table S3).

From a fundamental perspective, we cannot infer causation of these patterns because experimental interventions in this system are ethically challenging. However, underlying mechanisms could operate as in other host–pathogen systems. Individuals occupying particular network positions may be intrinsically or behaviourally disposed to increased exposure or susceptibility to infection. Alternatively, infection may lead to an individual's occupancy of a particular

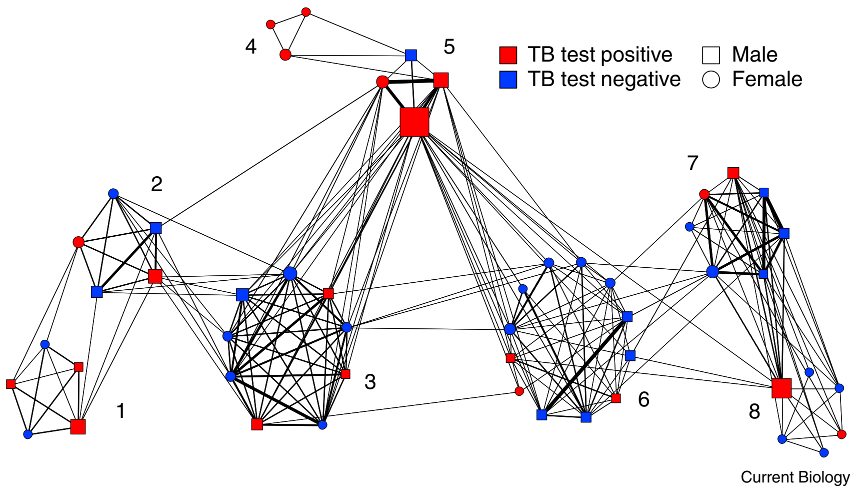

Figure 1. Social network and tuberculosis test outcome in a population of wild badgers.
Nodes represent all tagged individuals (*n* = 51) and are coloured according to the outcome of two live diagnostic tests for TB. Numbers represent social groups. Nodes are arranged to correspond with the spatial configuration of the eight social group territories but the proximity of nodes to one another is illustrative and has no spatial relevance. Thickness of the lines is proportional to degree centrality and the size of the nodes is proportional to among-group flow-betweenness. For underlying procedures, data and analyses see the Supplemental Information.

position because of social exclusion, or because the pathogen itself alters behaviour.

From an applied perspective, the importance of social structure to epidemiology and disease control is manifest [2], though counter-intuitive outcomes of common-sense approaches to wildlife disease control are also evident. Targeted removal of adult vampire bats, *Desmodus rotundus,* resulted in adverse outcomes for rabies control as juveniles and sub-adults were more important for transmission [6]. Tasmanian devil *Sarcophilus harrisii* social networks allow devil facial tumour disease to spread rapidly from any infected individual [7], hence culling of infected devils failed to reduce population impacts [8]. Our findings may help explain some of the complexity of TB epidemiology in group-living badgers. In this undisturbed network, TB+ individuals were socially isolated from their own groups whilst occupying influential positions in terms of flow, which we have related to disease transmission, across the population. Animals in such a position are therefore likely to make a disproportionately low contribution to spread within groups but a disproportionately high contribution to spread among groups. Although this distinctive network position was associated with infection, it does not conform to intuitive expectations of overall high centrality for ‘super-spreaders’ of infection [9]. Rather, these individuals might be considered ‘spread-capacitors’, because they are passive components in the network that may hold and discharge infection but which may stabilize flow. Social stability in badger populations is thought to mitigate disease spread [10], perhaps by maintaining the distinctive position of these individuals. Given that culling perturbs social structures and has been linked to increases in TB prevalence in badgers [5], the social and pathological characteristics of infected individuals indicate their network positions as especially influential in the outcome of interventions. In particular, vaccination has the potential to disrupt disease flow, without perturbing network structures.

Supplemental Information
Supplemental Information includes data, experimental procedures and three tables and can be found with this article at http://dx.doi.org/10.1016/j.cub.2013.09.011.

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