1. INTRODUCTION
The immune system is the evolutionary response to selective pressure from parasites and pathogens. Although vertebrates have both adaptive and innate immune responses, the vast majority of animal species rely upon the innate immune response. The innate immune system is costly to activate (Moret & Schmid-Hempel 2000) and costly to evolve (Kraaijeveld & Godfray 1997). Given these costs, particularly in the case of the former, it is unsurprising that the innate immune system exhibits plastic responses to perceived environmental threats, in the same way that phenotypic defences respond to environmental challenges.
activation, and total PO was assayed after activation of the proPO with chymotrypsin to produce active PO. For PO measurements, reaction mixtures contained 20 μl of haemolymph solution (dilution 1/20; haemolymph/sodium cacodylate/CaCl₂ buffer), 140 μl of distilled water, 20 μl of phosphate buffer saline (PBS: 8.74 g NaCl; 1.78 g Na₂HPO₄, H₂O₂, 1000 ml distilled water; pH 6.5) and 20 μl of L-dopa solution (4 mg per millilitre of distilled water). For total PO measurements, the 140 μl of distilled water contained chymotrypsin (0.07 mg ml⁻¹) and the mixture was incubated for 5 min at room temperature before reading the enzymatic activity. The reaction was allowed to proceed at 30 °C in a microplate reader (Versamax, Molecular Devices) for 40 min. Readings were taken every 10 s at 490 nm and analysed using SOFTmaxPRO 4.0 software (Molecular Devices). Enzyme activity was measured as the slope (Vmax value) of the reaction curve during the linear phase of the reaction (Barnes & Siva Jothy 2000).

Data were analysed with a full-factorial MANOVA (table 1) with group (social versus solitary) and colony as fixed factors to examine differences in the following dependent variables: antimicrobial activity, measured as the diameter of the zone of inhibition in mm (ZI), PO, and total PO. Data fulfilled the assumptions of the test. Some animals died during the experiment, reducing sample size to a total of 34 solitary and 40 social animals. Data were analysed with SPSS16 for MacOS X.

3. RESULTS
There were significant interactions between colony and social context. Animals from colony 1 exhibited an increase in anti-bacterial activity and total PO in social situations, whereas animals from the remaining two colonies showed the opposite effect (ZI: F(2,68) = 4.329, p = 0.017; total PO: F(2,68) = 3.672, p = 0.031). However, there was no significant interaction effect for PO activity (F(2,68) = 2.114, p = 0.129).

There were significant effects of group size on immune function (figure 1). Animals kept in social groups had 30 per cent higher total PO activity (F(1,68) = 12.769, p = 0.001; figure 1) and 36 per cent lower anti-bacterial activity (F(1,68) = 4.624, p = 0.035; figure 1) than animals kept on their own. There was no effect of social context on total PO activity (F(1,68) = 0.010, p = 0.922).

4. DISCUSSION
Social context elicits phenotypic plasticity in immune function in adult workers of the eusocial bumble-bee. Previous studies have demonstrated the impact of social context during larval development on either adult or late-instar immune function and resistance to parasites in insects (see §1). Our results suggest that such plasticity, or density-dependent prophylaxis, can also be elicited over very short timescales in adult insects. This significantly broadens the potential importance of DDP in understanding the dynamics of epidemiology and mortality in insect–pathogen systems.

Recent work suggests that the main frontline defence in insect immunity is the prophenoloxidase system, with anti-microbial peptides functioning to ‘mop up’ any remaining parasites or pathogens after the PO response (Haine et al. 2008). In our experiment, animals in social groups had significantly higher PO, indicating that groups are perceived as an increased pathogen/parasite threat and responded to by increasing frontline defences. This is in line with theories suggesting that sociality goes hand in hand with an increased disease threat (Alexander 1974). In addition to this increase in PO there was a decrease in antimicrobial peptides, providing further evidence for a physiological trade-off between these two branches of the immune system ( Cotter et al. 2004), which may be due to competition for limiting protein resources (Povey et al. 2009).

An alternative explanation for our results might be that changes in immune function are a response to the stress of being in a group of a particular size (Steinhäus 1958). However, animals did not show general depression of their immune system either in the social or the solitary context (in each case, one branch of the immune system was upregulated and...
the other downregulated), as would be expected if ‘stress’ were the cause (Reilly & Hajek 2008). Similarly, although workers in social groups compete for reproductive dominance (Honk et al. 1981), this is unlikely to lead to similar immune changes in dominant and subordinate animals (Sapolsky 2004), and because our samples were taken at random with respect to dominance from the social groups it is unlikely to be an explanation for our results.

Previous work suggested that DDP would be absent in social insects due to the plethora of alternative protective systems, and the fact that, by definition, social insects live in constant social conditions (Pie et al. 2005). However, both annual and perennial social insect societies go through significant population fluctuations. Our results suggest that, in such societies, adult animals can modulate their base immune function in an apparently adaptive way. Recent work found that immune function as measured by PO and haemocytes increased in bumble-bee workers as the colony aged (and increased in density) (Moret & Schmid-Hempel 2009). Our results provide a mechanism to explain this pattern.

To conclude, our results suggest that sociality may have selected for plasticity in the immune system, or DDP, in adult insects. This has implications both for the design of experimental studies of innate immunity, and for our understanding of the impact and epidemiology of parasites in the context of a socially variable host background.

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