

# Weak queen or social contract?

SIR — There may be a simpler explanation for the experiment that Reeve and Nonacs reported as evidence for social contracts in wasps<sup>1</sup>. Reeve and Nonacs observed increased aggression towards dominant alpha queens by beta queens when eggs were experimentally removed from the nest, and they interpret this as evidence for retaliation against alpha queens for eating eggs laid by the beta queen. Another interpretation consistent with these results is that the beta queen infers from the empty brood cells that the alpha queen is weak and might be vulnerable to a challenge. This would result in the observed escalated aggression by the beta queen and interference with the alpha queen's attempts to lay eggs, particularly by beta queens who are nearly as big as the alpha queen. This hypothesis also fits with West-Eberhard's finding<sup>2</sup> that alpha queens limit the reproduction of beta queens by restricting access to empty cells, as only the alpha queen begins new cells.

The weak-queen hypothesis is simpler than the social contract hypothesis because the former assumes only that the beta queen perceives that the cells are empty, and therefore that there is a problem with the alpha queen. The social contract hypothesis assumes that the beta queen perceives that the cells are empty, recognizes that some of those cells contained her eggs, and that she further assumes that the alpha female ate the eggs. Furthermore, she fails to recognize that most of the eggs the alpha queen ate she also laid. The weak-queen hypothesis also accords better with what we know about egg recognition. Eggs are thought to be recognized for only the brief time during which they are guarded<sup>2,3</sup>. In this species eaten eggs were on average 11.4 minutes old, and females guarded their eggs for up to 20 minutes<sup>2</sup>.

Another advantage of the weak-queen hypothesis is that it provides a more natural explanation of why the beta and not the alpha queen increases aggression. The alpha queen would not increase aggression as she is already the dominant queen. Under the social contract hypothesis, the alpha queen encountering empty cells formerly containing eggs could also think that the social contract had been broken by the beta queen. It would then follow that the alpha queen should also increase aggression when eggs are experimentally removed.

The beta queen was observed by Reeve and Nonacs to increase aggression towards the alpha queen in July and not

in June. The social contract hypothesis explains this difference as resulting from the timing of laying of reproductive eggs, which is more likely to be in July than in June. According to this interpretation, beta queens are selected to care about the parentage of eggs destined to become reproductives and not of eggs destined to become workers. One difficulty with this interpretation is that it relies on the untested assumption that workers can predict the eventual caste of eggs in the face of unpredictable future effects of individual nest conditions<sup>1,4,5</sup>. There is another, simpler interpretation. Early in the season females fight to establish rank so absolute levels of aggression are high, and differences in aggression among females are small. Therefore there is not much room for experimental change in aggression levels. Later in the season, as rank becomes better established, the alpha and beta queens diverge more in behaviour, ovarian development and hormone titres<sup>6,7</sup>. This provides more room for an increase in aggression by beta queens in an experiment. The beta queen's behaviour changes less in June because in June hormone titres of the beta female are still high and more similar to those of the alpha queen<sup>2,8</sup>. In July, when provided with the stimulus to lay eggs (empty cells<sup>2</sup>), more of the hormone that governs both egg-laying and aggression (juvenile hormone) is produced, resulting in increased aggression.

Removal of pupae did not elicit aggression by the beta queen. However, pupae are often naturally removed in attempts to rid the brood of parasites such as *Chalcoela iphitalis*, whose larvae can move from cell to cell, destroying all pupae<sup>9</sup>. This makes it unlikely that empty pupal cells would be an indication of a weak queen, so this result is consistent with both hypotheses.

In sum, although the social contract hypothesis is intriguing and possibly true, the weak-queen hypothesis explains all the observed phenomena in a simpler way.

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