

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^{1,4,5}. 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^{6,7}. 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^{2,8}. In July, when provided with the stimulus to lay eggs (empty cells²), 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 pupae⁹. 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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REEVE AND NONACS REPLY — We disagree that the weak-queen hypothesis is more parsimonious than our social contract hypothesis¹; more important, several results strongly contradict the former.

First, the weak-queen hypothesis assumes that the beta queen perceives that the cells are empty, assumes that empty cells reflect an unspecified 'weakness' in the alpha queen, with beta failing to remember that these cells contained eggs immediately before both

queens were removed from the nest and continuing to perceive this 'weakness' despite normal behaviour by the alpha queen. Thus both hypotheses are complex. Strassmann argues that our hypothesis cannot easily explain the observation that queens usually stop guarding their own eggs and refrain from eating their nestmate's eggs only minutes after such eggs are laid². However, a restricted period of guarding or egg eating does not imply that queens cannot discriminate between their own and their nestmate's eggs beyond this period. Indeed, nest-switching experiments suggest that queens can discriminate among eggs of varying relatedness to them hours to days after such eggs have been laid¹⁰.

Second, if the weak-queen hypothesis were correct, we should have seen at least some increase in aggression by the beta when worker-destined eggs were removed (as this also creates empty cells and thus should indicate a weak alpha). In fact, beta's aggression dropped slightly after removal of such eggs. Strassmann argues that the lack of increase in beta's aggression resulted only from beta's high juvenile hormone titres early in the summer, which makes betas nearly as aggressive as alphas, by contrast to later in the summer when betas are less aggressive and thus capable of displaying greater net increases in aggression. But this explanation cannot apply to our results since natural rates of beta aggression in our early (worker-egg) colonies (10.4 acts per hour) were not different from those of later (reproductive-egg) ones (10.2), probably because dominance hierarchies had stabilized even in the former. These data preserve the evolutionary hypothesis that selection favours enhanced protectiveness of eggs that are likely to be reproductive-destined late in the season.

According to the weak-queen hypothesis, beta's aggression should be relatively low when alpha tries to lay eggs in treatment nests, because this should indicate that alpha is less afflicted by the unspecified 'weakness'. In fact, beta is more aggressive when alpha tries to lay eggs.

We have devised a critical test of the hypotheses. According to the weak-queen hypothesis, an alpha that replaces eggs at a high rate after egg removal treatments should be viewed by beta as less afflicted by the weakness than an alpha that replaces eggs at a low rate, and thus the former alphas should be treated less aggressively than the latter. According to the social-contract hypothesis, betas should be more aggressive to queens that lay replacement eggs at higher rates, as it is these alphas that will be perceived as most flagrantly 'cheating' on the social contract. The result is decisively in favour of the social con-

tract. In treatment colonies, betas exhibited larger increases in aggression toward alphas that laid replacement eggs at high rates (+16.9 acts per hour) than toward alphas that laid replacement eggs at low rates (-7.4; $P < 0.05$).

The weak-queen hypothesis is interesting in its own right and should be tested in other contexts, but it can be rejected as an explanation for our results. Social wasp queens indeed seem to maintain their social contract over reproduction by close monitoring of relative reproduction coupled with the threat of aggressive retaliation against cheating.

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K/T melt glasses

SIR — In our recent paper¹, we used the chemical composition of a melt rock from the Chicxulub structure to confirm Chicxulub's identity as an impact crater and as the source of impact melt spherules found at the Cretaceous/Tertiary (K/T) boundary in Haiti. We did this by first demonstrating that the quenched molten portion of the melt rock does not lie on igneous fractionation paths and thus is not likely to be a volcanic product. Second, we showed that this composition lies on a chemical mixing trend seen among K/T boundary impact melt glasses, and thus concluded that both sets of samples were probably produced by the same impact event. Although these results have since been substantiated by other groups using different methods^{2–4}, Schuraytz and Sharpton⁵ in Scientific Correspondence suggested that our results were fortuitous for reasons we address here.

Schuraytz and Sharpton⁵ drew attention to the potential effects of hydrothermal alteration on the composition of the groundmass. We considered these: