

BSE and vCJD are caused by the same prion strain. Taken together with the temporal and spatial association of vCJD with BSE but not with scrapie or other animal prion diseases, and BSE transmission studies in macaques¹¹, this strongly suggests that vCJD is caused by BSE exposure. The theoretical possibility that both BSE and vCJD arise from exposure to a common unidentified source appears remote.

The production of a distinct molecular strain type on transmission of vCJD to mice expressing valine 129 human PrP suggests that BSE transmitted to humans of this genotype might produce a similar strain. Such cases may differ in their clinical and pathological phenotype to vCJD, but could be identified by PrP^{Sc} typing.

Although it has been argued that the species barrier resides in PrP primary structure differences between donor and host¹², our data emphasize that strain type can be as important. As prion propagation involves interactions between PrP^{Sc} and host PrP^C, and strains are associated with differences in PrP conformation and glycosylation^{2,13}, such PrP interactions may be most efficient if the interacting proteins are not only of the same sequence but have similar conformational preferences and glycosylation. Mismatch of codon 129 between inoculum and HuPrP^{+/+} Prn-p^{0/0} mice does not significantly affect CJD transmission, but this could differ for BSE. All vCJD cases have been 129MM genotype (ref. 14 and unpublished data). Although our 129VV mice are much less susceptible to BSE than to typical CJD, suggesting a substantial species barrier, 129MM human PrP mice could be more susceptible.

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'Male-stuffing' in wasp societies

Intracolony aggression within and between castes of social insects is common^{1–3}. We have observed an unusual aggressive interaction between nestmates of the paper wasp *Polistes dominulus*. In response to foragers returning to the colony, females (workers) initiate aggressive encounters with males culminating with the male being forced head-first into an empty nest-cell ('male-stuffing'). 'Stuffed' males are unable to feed, so the behaviour seems to ensure that food is preferentially channelled to larvae, which are likely to be more closely related to the workers than are the adult males.

We observed two categories of stuffing. 'Initial stuffing' (Fig. 1) began with antenna-to-antenna contact and was followed by grappling, biting, and sting-threats. The aggressor then forced the recipient head-first into an empty cell. 'Repeated stuffing' was characterized by biting and pushing the abdomen of an individual whose head and thorax were already inside a cell.

We studied the behaviour by transcribing and analysing 26 hours of videotape. We saw stuffing behaviour only in colonies containing males ($n=5$ colonies) and not in those without ($n=6$ colonies; sexed by antennal morphology²; $\chi^2=21$, $P<0.001$). Stuffing was directed exclusively at males, despite their being greatly outnumbered by females (1:4.21) in colonies of both sexes (binomial test, $P<0.0001$). Of 66 stuffing events, 46 were directed at males from that colony (identified by marking them at eclosion); the remainder were of unknown origin. Queens ($n=5$) did not stuff males (0/66 events; binomial test, $P<0.1$). All stuffing was done by workers other than the returning forager.

Initial stuffing occurred soon after the return of a forager, whereas repeated stuff-

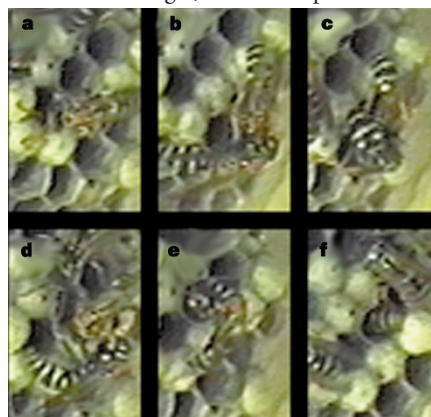


Figure 1 Initial male-stuffing. **a**, Male on the comb. **b**, Female (worker) approaches and antennates him, **c**, followed by biting and sting-threats. **d**, She stuffs him into an empty cell, **e**, and pushes on his abdomen. **f**, Male in the cell.

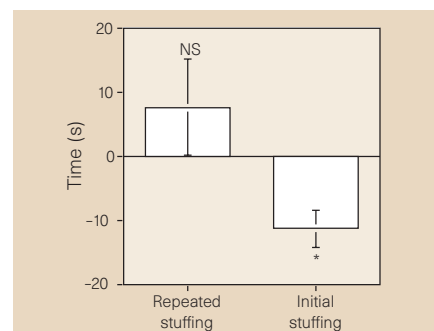


Figure 2 Difference between the time from most recent male arrival until stuffing and half the average interval between returns. A value of 0 is expected if male-stuffing is random with respect to arrivals. Initial stuffing ($n=32$) occurred shortly after a nestmate returned ($\bar{t}=18.86 \pm 2.89$ s; Wilcoxon signed-rank test: $Z=-3.20$, $*P<0.01$), but repeated stuffing ($n=34$) occurred randomly with respect to arrivals ($\bar{t}=39.88 \pm 7.51$ s; $Z=-0.18$, $P>0.8$; NS). Means \pm s.e.m.

ing occurred at random times (Fig. 2). Males that had been repeatedly stuffed remained in cells 6.35 times longer ($\bar{t}=384.29 \pm 43.01$ s; mean time \pm s.e.m.) than the mean time between forager arrivals ($\bar{t}=60.53 \pm 2.25$ s; $n=833$). Thus, stuffing may function to preclude males from gaining access to resources gathered by the workers.

Limiting food consumption by males may maximize the inclusive fitness of workers, who should direct their help towards closely related kin^{4,5}. Feeding future reproductive females provides a larger fitness pay-off than feeding adult males⁶. Workers from a colony containing one singly mated queen have a relatedness to sisters of 0.75. Workers are only related by 0.25 to brothers, 0.375 to nephews (worker-produced males) and are unrelated to immigrant males.

Assuming that female larvae are present, workers are more closely related to reproductive-destined larvae than to adult males. Even in circumstances where workers are, on average, equally related to male and female nestmates (such as brothers and half-sisters when the queen has mated more than once), feeding needy larvae may provide a larger inclusive fitness pay-off than feeding adult males, which can forage for themselves. Preferential channelling of resources to larvae, by stuffing males, may maximize the genetic self-interest of worker wasps.

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