separate components to the jumping response because a similar trend was observed in the syringe control. Insect-associated volatile cues are important triggers for jumping behaviour, but it is air movement that influences the direction of the jump.

Directional jumping in response to the close proximity of a potential host may increase the probability of the infective juvenile contacting it. Jumping appears to be part of a range of behavioural traits, including standing and foraging at the soil surface, by which some nematodes are able to exploit ground-dwelling insects as hosts. Understanding the role of jumping in host search behaviour has implications for the successful use of this nematode in the biological control of insect pests[6].

**James F. Campbell*, Harry K. Kaya†**
*Departments of *Entomology, and †Nematology, University of California, Davis, California 95616, USA*
*e-mail: jfcampbell@ucdavis.edu*

1. Reed, E. M. & Wallace, H. R. *Nature* **206,** 210–211 (1965).
2. Campbell, J. F. & Gaugler, R. *Behaviour* **126,** 155–169 (1993).
3. Maggenti, A. *General Nematology* (Springer, New York, 1981).
4. Kaya, H. K. & Gaugler, R. *Annu. Rev. Entomol.* **38,** 181–206 (1993).
5. Campbell, J. F., Lewis, E., Yoder, F. & Gaugler, R. *Parasitology* **113,** 473–482 (1996).
6. Gaugler, R., Lewis, E. & Stuart, R. J. *Oecologia* **109,** 483–489 (1997).

# Non-fertile sperm delay female remating

Sperm competition is thought to be responsible for the tremendous inter- and intraspecific variation in sperm number[1] and size[2]. But why several animals produce a range of sperm types[3,4], some of which are incapable of fertilizing the female's eggs[4], has remained unexplained for nearly 100 years[5]. We have found that non-fertile sperm protect a male's reproductive investment by delaying female remating in the polyandrous green-veined white butterfly, *Pieris napi* (Pieridae).

Lepidoptera have two distinct sperm types: fertile 'eupyrene' sperm and non-fertile 'apyrene' sperm, which lack nuclear material[6]. Apyrene sperm have a distinct developmental pathway, and so cannot be considered aberrant[6]. They are shorter, thinner and contain less mitochondrial material than eupyrene sperm[6]. Both types are transferred to the female at mating, with more than 90% being apyrene sperm[7], and both migrate to the site of sperm storage, the spermatheca.

The high motility of apyrene sperm suggests that they may aid the transfer of eupyrene sperm, in which case there should be a constant ratio between the two sperm types, whereas males actually vary the proportion considerably[7]. Alternatively, apyrene sperm may represent nutrients for the female, zygote or eupyrene sperm in storage[8]. This is also unlikely, because nutrient donations in paternally investing species are transferred in a non-ejaculate part of the spermatophore (the sperm-containing packet)[9]. Another possibility is that apyrene sperm may be involved in sperm competition[10]. When mating with females who have already been inseminated, apyrene sperm could interfere with rival males' sperm. They may also influence female receptivity, filling the spermatheca and delaying female remating.

We tested this last hypothesis. Females were mated to virgin ($n=22$) or mated males ($n=14$). If apyrene sperm delay remating, we would expect females with more apyrene sperm in storage not to remate. Females were allowed to remate at will for up to ten days after mating (females rarely remate after this time[9]). The two sperm types in the spermatheca originating from the first male were counted, either when the female remated or after ten days if the female did not remate.

We found that female receptivity is related to the number of apyrene sperm in storage. As predicted, remating females have fewer apyrene sperm already present in their spermatheca than females who did not remate, whereas there was no difference in the number of fertilizing sperm stored (Fig. 1). Female remating is also related to male mating status. Females receiving smaller spermatophores from mated males ($3.6\pm0.34$ (s.e.) mg versus $6.5\pm0.25$ mg; $F_{(1,63)}=48.1$, $P<0.001$) remate more (12 out of 14 versus 13 out of 22, $\chi^2=3.97$, $P<0.05$, 1 d.f.) and sooner ($3.4\pm0.45$ versus $5.5\pm0.55$ days, $t=2.95$, $P<0.01$, 24 d.f.) than females receiving larger spermatophores from virgin males. Mated males, despite transferring smaller spermatophores, provide more eupyrene sperm than do virgin males ($8{,}469\pm1{,}046$ versus $5{,}757\pm911$, $t=2.16$ on log-transformed data, $P<0.05$), as in the related *P. rapae*[7], but do not transfer more apyrene sperm ($44{,}954\pm5{,}622$ versus $49{,}980\pm4{,}475$; $t=0.83$, $P>0.4$, 62 d.f.).

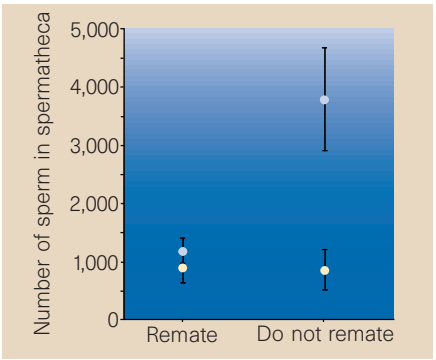


**Figure 1** Relation between number of apyrene sperm stored and female remating. Females that do not remate have more apyrene sperm in storage (pale blue circles; log-transformed data, $F_{(1,32)}=5.33$, $P<0.01$). The mating status of her first partner (whether mated or virgin) has no effect on apyrene storage ($F_{(1,32)}=0.05$, $P>0.8$) and there is no interaction between male mating status and female remating ($F_{(1,32)}=0.01$, $P>0.9$). There is no difference in eupyrene sperm number (pale yellow circles; $F_{(1,32)}=1.31$, $P>0.2$), no effect of male mating status ($F_{(1,32)}=2.50$, $P>0.1$) and no interaction ($F_{(1,32)}=0.02$, $P>0.9$). Bars show standard error. There is a positive correlation between days until remating and number of apyrene sperm in the spermatheca (females mated to virgin males, $r=0.64$, $P<0.02$; to mated males, $r=0.63$, $P<0.03$), but no relationship with the number of eupyrene sperm in storage (females mated to virgin males, $r=0.32$, $P>0.3$, $n=13$; to mated males, $r=0.13$, $P>0.7$, $n=12$).

The relation between time before remating and number of apyrene sperm stored indicates that the induction of non-receptivity in females does not depend on a threshold level of apyrene sperm. The quantity of stored apyrene sperm is more variable than the numbers delivered (adjusted coefficient of variation: 111 versus 7). It is not clear whether this variation is due to differences in quality or persistence of apyrene sperm in storage, or in the tendency of females to store apyrene sperm. Nevertheless, controlling for the effect of male mating history, we find that females that store more apyrene sperm do not remate.

Males may be using apyrene sperm to exploit a female system designed to monitor sperm numbers in storage to ensure maximum fertility. Apyrene sperm may be less costly to produce than eupyrene sperm, or more efficient in reducing female receptivity. Instead of containing large amounts of nucleate sperm, males' ejaculates consist mainly of anucleate sperm, delaying female remating and hence reducing the potential for sperm competition.

**Penny A. Cook*, Nina Wedell†**
**School of Health, Liverpool John Moores University, 79 Tithebarn Street, Liverpool L2 2ER, UK*
*e-mail: p.a.cook@livjm.ac.uk*
*†Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden and Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia*

1. Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. *Proc. R. Soc. Lond. B* **264,** 1793–1802 (1997).
2. Pitnick, S., Spicer, G. S. & Markow, T. A. *Nature* **375,** 109 (1995).
3. Sivinski, J. *Fla. Entomol.* **63,** 99–111 (1980).
4. Snook, R. R. & Karr, T. L. *Curr. Biol.* **8,** 291–294 (1998).
5. Meves, F. *Arch. Mikrosk. Anat. EntwMech.* **61,** 1–82 (1902).
6. Friedländer, M. *J. Insect Physiol.* **43,** 1085–1092 (1997).
7. Cook, P. A. & Wedell, N. *Proc. R. Soc. Lond. B* **263,** 1047–1051 (1996).
8. Riemann, J. G. & Gassner, G. *Ann. Entomol. Soc. Am.* **66,** 154–159 (1973).
9. Wiklund, C., Kaitala, A., Lindfors, V. & Abenius, J. *Behav. Ecol. Sociobiol.* **33,** 25–33 (1993).
10. Silberglied, R. E., Shepherd, J. G. & Dickinson, J. L. *Am. Nat.* **123,** 255–265 (1984).