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Backhaus et al. *reply* — Avenel *et al.* have suggested a mechanism that might explain the recently discovered[1] metastable π-state in a superfluid ^{3}He weak-link array. We are pleased that our experiment is leading to new ideas that may extend the understanding of weak-link arrays. We agree with Avenel *et al.*'s comment that, when the individual apertures are in a (short coherence length, low temperature) hysteretic regime, collective phenomena quite distinct from single weak-link behaviour might be observed. Nevertheless, in the temperature regime in which the coherence length is comparable to the aperture dimensions, we have shown that the collective behaviour of the array is similar to that of a single weak link[2,3].

Although we are gratified that the mechanism proposed by Avenel *et al.* for the π-state expands on our previous conjecture[1] that internally trapped circulating currents could be involved in its existence, we do not believe that it is the only possible explanation. This is because agreement between a given data set and a numerical simulation, using a model with several adjustable parameters, represents a check that the model is consistent with the data, but does not qualify as a proof of the model[4]. Therefore, we cannot say to what extent their model represents physical reality better than other theories of the π-state that have been recently proposed[5].

However, several aspects of their simulation disagree with our experimental observations. In particular, the model presented by Avenel *et al.* does not seem to conserve energy in the oscillator, contrary to our experimental results. Their model predicts that the $I(\phi)$ relation should extend beyond $\phi=\pi$ before the onset of the π-state. In contrast, the collapse into the π-state occurs at $\phi<\pi$. Finally, as shown in their Fig. 1c and supported by our own simulations, their model leads to metastable states at positions other than π, a feature also in contradiction to the data.

We hope that Avenel *et al.* will continue to refine their simulations to make predictions that could lead to a conclusive test of their underlying model.

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How and why a parasitic nematode jumps

Jumping is an unusual behaviour performed by some nematode species[1], but has been seen only in the infective or phoretic stages of species associated with insects[1–3]. This correlation suggests that jumping may be involved in the location of insect hosts. We find that infective juveniles of the insect-parasitic nematode *Steinernema carpocapsae*, when standing on their tails, are triggered to jump by the presence of host-associated volatile cues, and that they tend to jump towards them. Directional jumping in response to information about insect proximity could be an adaptation for host attack by this parasite.

S. carpocapsae is a lethal endoparasite capable of infecting a broad range of insect species[4]. The infective juvenile, which emerges from a depleted host cadaver to seek out a new insect to infect, is the only free-living stage. Infective juveniles tend to be found at the soil surface[5], and use an ambushing search strategy in which they stand on their tails and attach to a passing insect[2]. They are more likely to be picked up by an insect when they are standing because of the reduced surface tension holding them to their substrate.

Jumping, which previously was inaccurately described[1], is initiated when a standing nematode quickly bends the anterior half of its body until its head region makes contact with the ventral side of its body. The two body regions appear to be held together by the film of water covering the nematode's body[1]. The nematode now has resistance to the bending of its body, so it can use its normal sinusoidal crawling behaviour to slide its body in a posterior direction, causing the loop to become progressively smaller and the bend in its body to become more acute.

Eventually, the body becomes so contorted that the cuticle on the dorsal side becomes extremely stretched and the cuticle on the ventral side kinks, generating sufficient force to break the surface tension forces holding the nematode to the substrate and propel it through the air. The forces generated by this jumping mechanism are sufficient to propel nematodes an average distance of 4.8 ± 0.8 mm (nine times the nematode's body length) and an average height of 3.9 ± 0.1 mm (seven times the nematode's body length).

If jumping behaviour has been acted on by natural selection to function in finding hosts by ambush, then we might expect it to be triggered by the presence of potential hosts, and for nematodes to jump towards the host. We found that *S. carpocapsae* infective juveniles standing on their tails responded differently to different types of information from the environment (Fig. 1). Nonspecific cues such as air movement, in this case associated with moving a syringe tip to within a millimetre of the infective juvenile or applying a puff of air through the syringe, triggered a small increase in jumping. The proportion of individuals jumping increased dramatically when more specific cues indicating the proximity of an insect were introduced. When the tip of a syringe containing larvae of the host *Galleria mellonella* (Lepidoptera) or adults of *Acheta domesticus* (Orthoptera) was introduced to standing infective juveniles, nearly all nematodes were induced to jump.

S. carpocapsae infective juveniles were able to change the direction of jumping in response to information from the environment (Fig. 1). Infective juveniles tended to jump towards the source of the air movement when air movements were small (syringe), but directionality was lost when they were large (puff of air), indicating that large air movements may inhibit the nematode from deriving directional information. When host cues were present, the nematodes tended to jump towards the source of the cues; however, there seem to be two

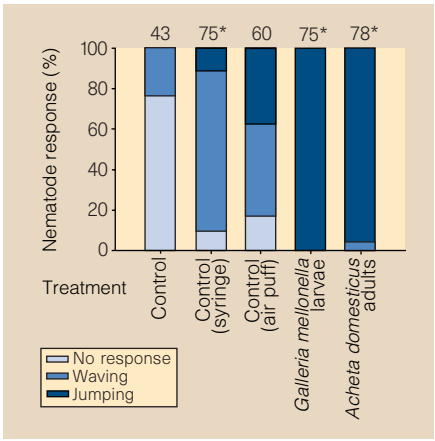

Figure 1 Influence of different cues on the initiation and direction of jumps of *Steinernema carpocapsae* infective juveniles. The following stimuli were presented by moving a Hamilton 10-ml gas-tight syringe to within 1 mm of a standing infective juvenile: control (no syringe); syringe (empty syringe); air puff (syringe was depressed to create a puff of air); or the syringe contained four individuals of either *Galleria mellonella* larvae or *Acheta domesticus* adults. Nematodes either remained in the straight standing posture (no response), waved back and forth while standing (waving), or initiated a jump (jumping). The proportion of individuals jumping towards the cues is shown at the top of each bar; numbers with stars are significantly different in jumping direction (contingency table analysis with chi-square tests at $P<0.05$). We tested 60 nematodes for each treatment.

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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].

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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 ± 0.34 (s.e.) mg versus 6.5 ± 0.25 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 ± 0.45 versus 5.5 ± 0.55 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.).

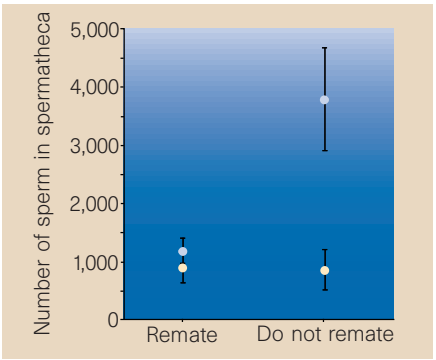

Figure 1 Relation between number of apyrene sperm stored and female remating. Females that do not remate have more apyrene sperm in storage (pale blue circles; log-transformed data, $F_{(1,32)}=5.33$, $P<0.01$). The mating status of her first partner (whether mated or virgin) has no effect on apyrene 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.

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