MATTERS ARISING

Myths and mad March hares

HOLLEY and Greenwood¹ claim that boxing in hares is the female's attempt to prevent mating, and that 'madness' is not a feature of March. The behaviour they describe as boxing I call rebuff². An unreceptive female lunges at a male that comes too close, usually from the semi-crouched threat position. Boxing between males establishes dominance³. In Germany the characteristic erect posture of two males feinting with the fore paws, 'Distanzgefecht' or real boxing in contrast to 'Brustkampf' the usual female rebuff, has been photographed in marked individuals^{4,5}. Dr E. Schneider (in litt., 2/9/84) recorded boxing at least 40 times, all male-male in the 16 bouts with sexes identified. In 17 rebuffs, 14 involved females. That no male-male boxing was recorded by Holley seems curious; perhaps his population was so isolated the males all knew their ranking.

Testosterone levels in English hares rise dramatically from February to April, so interaction between males is likely to peak in March, as do daylight sightings of adult hares in Norfolk⁶. In New Zealand where turf remains short throughout the year, hare sightings peak in September (the equivalent of March). Hence I do not agree that male 'mad March hares' are a myth, or that female hares do the boxing.

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Sperm sharing in *Biomphalaria* snails

SINCE 1968, as an inference from observations published later¹, I hypothesized that a simultaneous hermaphrodite snail with a planorbid-type reproductive system could transfer sperm from a donor to a recipient snail. Such hypothesis, tested in numerous crossing experiments with Biomphalaria glabrata, proved untenable. The report by Monteiro, Almeida and Dias² led me to repeat my former (unpublished, of course) experiments, this time strictly following the procedure described by those authors. I had previously performed unsuccessfully similar experiments at the same laboratory of the University of Brasilia, and with the same strain of B.

glabrata successfully handled by these authors.

Concerning B. tenagophila, in which transference of sperm from donor to recipient through an intermediate snail is asserted to have occurred in 20 out of 70 experiments (about 28%), I carried out tests with 47 trios, using the same strains that were used by the mentioned authors: NB-JO-JO (14), NB-JO-BH (9), NB-BH-JO (10), JP-JO-JO (7), JP-BH-JO (7). These trios correspond to the most successful combinations mentioned by Monteiro et al., since transference of sperm is said to have occurred in 18 experiments (about 38%). In my trials, however, not even a single candidate recipient produced any embryo resulting from fertilization by donor's sperm during a period of 100 days from the 'intermediate-recipient' pairing. The only explanation that occurs to me for the alleged transference of sperm is that there was confusion of albino 'intermediate' and albino 'recipient' during the mating period, when similar snails were paired and separated every day.

Another disputable statement made by Monteiro et al. is that 'crossbreeding between B. tenagophila and B. occidentalis is common in the laboratory'. In my description of the latter as a new species³, I emphasized that it is indistinguishable from B. tenagophila by the shell characteristics, and showed that the two species differ morphologically in some features of the genital system and are separated by absolute reproductive isolation. The latter characteristic was now confirmed, when I failed to interbreed B. occidentalis from Sena Madureira (SM) and B. tenagophila to form the trios SM-BH-BH, SM-JO-BH and SM-JO-JO, for a complete lack of hybridization between SM-BH (10 couples) and SM-JO (10 couples). My explanation of the successful results mentioned by Monteiro and colleagues is that in their experiments B. tenagophila was mistaken for B. occidentalis.

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MONTEIRO et al.¹ describe sperm sharing in simultaneously hermaphroditic *Biomphalaria* snails, a strategy inconsistent with most models of mating systems. We suggest that this represents 'cheating' in a sperm-trading mating system, such as that found in the opisthobranch, Navanax inermis²⁻⁴, and predicted for pulmonate gastropods⁴.

Recent theories of mating systems are

based on Bateman's principle⁵, which states that fecundity of females is limited by the energy available for egg production, and that of males by access to females or eggs. Therefore, simultaneous hermaphrodites should mate 'not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs)⁶. That is, they should trade eggs, as has been described for Hypoplectrus, a serranid fish⁷. In contrast, sperm sharing represents 'a strategy enabling the snail to receive much sperm from its partners, when it is acting as a functional female, while transferring relatively few spermatozoa of its own'1. This suggests that Biomphalaria are trading sperm rather than eggs.

In a sperm-trading mating system, individuals mate as males not so much to fertilize eggs as to receive sperm to fertilize their own eggs (as in Navana x^{2-4}). Comparison of the mating systems of Hypoplectrus and Navanax suggests that the risk of gamete loss (rather than the energy invested in gametes) determines the 'preferred' sexual role. Simultaneous hermaphrodites should trade sperm, rather than eggs, wherever sperm are at a greater risk of loss before fertilization³. In Biomphalaria, eggs are assured of fertilization because females can self-fertilize if necessary⁸. However, copulating as a male does not guarantee access to eggs since Biomphalaria store foreign sperm and digest the $excess^{9,10}$. To act as a female should therefore be the preferred role in Biomphalaria.

Sperm sharing represents a way of reciprocating with a partner without producing any (or as many) sperm of one's own, as these may be digested rather than used in fertilization. It is a way of 'cheating' as a male. Sperm sharing will not harm the female unless the female received its own sperm back from its partner. We expect that mechanisms to prevent this should exist since cross-fertilization is preferred in *Biomphalaria*¹¹.

Monteiro *et al.*¹ suggested that sperm sharing might represent an evolutionarily stable strategy related to a bias towards female function. However, *Hypoplectrus*, which trades eggs, has sex allocation biased toward female function¹² and Bateman's principle¹³ cannot explain why an animal should transfer foreign sperm to a partner.

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