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LEER EN ESPAÑOL

The persistent embrace of onychophorans: What determines copulation duration in velvet worms?

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ABSTRACT: **In the only onychophorans mating that has been photographed, instead of fleeing, the couple remained together despite being manipulated. Why? The duration of copulation in onychophorans is possibly controlled by the female, larger and stronger than the male, probably with the participation of dopamine and γ-aminobutyric acid. Insemination through the body wall can be a male mechanism to overcome female defenses.**

KEYWORDS: reproductive mechanism, onychophoran mating, insemination, spermatheca.

In the only pairing of onychophorans that has been photographed (Figure 1), the couple remained together for more than 15 minutes, even though they were captured and manipulated. Why did they not separate and fled?

FIGURE 1. **Australian onychophorans mating: the male inserts the spermatophore vaginally with his head. Right: detail of the male´s head with its spermatophore; drawing by J. Monge Najera based on photographs by Tait and Norman (2001).**

In invertebrates, the decision of when to end copulation can be taken equally by both parties, but frequently one dominates. For example, the male can strongly hold the female (Thornhill & Sauer, 1991) and adjust the amount of semen and nutrients it provides, controlling the duration of the copulation (Bretman, Westmancoat, & Chapman, 2013); if the female is "of lower quality", he shortens the copulation and shares less nutrients (Bonduriansky, 2001).

The fact that onychophoran females are often larger than males suggests that they have greater control. They can take several measures, from preventing the male from placing the spermatophore in their body, to diminishing the effect of spermatozoa, by mixing his sperm with the sperm of other males, by hindering their advance, or even by destroying them in the spermatheca.

This would explain why they mate with multiple males, as observed by Curach and Sunnucks (1999); why the vagina is strongly muscular and ciliated, as reported by several authors (e.g. Manton, 1938, Brockmann, Mummert, Ruhberg, & Storch, 1999); why there is no open communication between the ovaries and the entry of spermatozoa, as found by Manton (1938); and why the ovaries have "accessory pouches" where Sherbon and Walker (2004) observed half-decomposed spermatozoa. Perhaps onychophoran males developed insemination through the body wall, just like some bugs (for bugs see Siva-Jothy & Stutt, 2003), because it allows them to overcome the female defenses, and not because the vagina is blocked by embryos, as others have believed (Tait & Norman, 2001).

In any case, in the Australian worm *Florelliceps stutchburyae*, Tait and Norman (2001) observed that copulation requires the female to keep the male's head in position (this species uses special head structures to place the spermatophore in the vagina). It is the female who controls if copulation occurs, and she also defines when it ends. Possibly, transfer of enough semen for a successful reproduction requires at least half an hour. The evolution of how long copulation lasts, and when it is justified to abort it, results from the relationship between the fundamental importance of fertilization, and the decision to separate from danger or another need.

Only rarely does a pair separate if the transfer of gametes is insufficient, and onychophorans probably control the copulation with DNA sequences that exist since the Cambrian and that we know from studies in other invertebrates (e.g. Crickmore & Vosshall, 2013). The mechanism is simple: the copula is dominated by a group of dopamine processing neurons. After the transfer of gametes is finished, another neuron group, constituted by interneurons "GABAergic", releases γ-aminobutyric acid, a neurotransmitter that causes the end of copulation. We suspect that, when the subject is studied, the mechanism in onychophorans will turn out to be that dopamine-GABA interaction, and that this interaction will explain the persistent "embrace" of onychophorans.

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