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Post-insemination associations between males and females in Diplopoda: A remark on Alcock's (1994) predictions of the mate-guarding hypothesis

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Abstract
Here I review the most common form of mate-guarding (prolonged copulation) in the Diplopoda. The ten predictions for mate-guarding in Insects are compared using Diplopod examples and evidence in favour of 7 of Alcock's (1994) predictions (1, 2, 3, 4, 5, 6, 8) was found. Future research on mate-guarding in the Diplopoda may test 2 untested predictions (7 and 10). The last prediction (9) cannot be tested as millipedes are non-territorial.

Keywords: diplopod; mate-guarding; mating; millipede; post-insemination

1. Introduction

Of the diversity of post-insemination associations between the sexes in the insects [1], prolonged copulations dominate in the diplopods [2-21]. In most species, males maintain genital contact far beyond the time needed only for insemination of the female. There is preliminary evidence for mating plugs where males transfer secretory materials that seal or hinder access to a female's reproductive tract [22]. There is no mate grasping and mate monitoring in the Diplopod as there is in the insects [1]. The only alternative hypothesis is the possible prevention of rival ejaculates from competing with sperm already donated to a partner. Sperm displacement may take the form of self-sperm displacement or mixing as was demonstrated in *Alloporus uncinatus* [13]. In the Diplopods the most competitive hypothesis is for mate guarding (to protect an already donated ejaculate). The key predictions pointed out by Alcock [1] are reviewed.

2. Materials and Methods

The 10 predictions from the Mate-guarding Hypothesis [1] were reviewed by looking for evidence from the Diplopods. Each of the original 10 predictions were dealt with and any supporting evidence for the prediction was sought for. Once any supporting evidence was found the next prediction was tested. If no evidence could be found in support of the prediction it was stated.

3. Results and Discussion

Prediction 1: Mate Guarding Occurs Only When Females Retain Their Receptivity Following Insemination

Records for multiple mating include the double mating performed in *Centrobolus* spp. where competition was determined by a 24hour re-mating interval [23]. Evidence for female retention of receptivity can be found in *Poratophilus diplodontus* which females mated up to five times in sequence with different males [22]. Indirect evidence in support of this prediction is also found in the correlation between second copulation durations and re-mating interval [22-23].

Prediction 2: A Males Capacity to Resist a Take-Over Influences His Readiness to Mate-Guard

The discernment of parallel copulator from coiled copulator indicated mate guarding strategies of how millipedes can resist take-overs [9]. The parallel copulator was less likely to resist a take-over compared to the coiled copulator. The coiling behaviour is thus a direct response to resist take-overs and indicative of a successful mate guarding.

Prediction 3: The Greater the Degree of Sperm Precedence, the Greater the Likelihood of Mate Guarding Second male sperm precedence correlates with copulation duration which in turn equates to higher reproductive success in *C. inscriptus* [23]. A similar finding was obtained for second male sperm precedence in the Spirostreptida [22]. Thus evidence exists for this prediction.

Prediction 4: Male-Biased Operational Sex Ratios (Osr) Are Associated With Intense Mate Guarding; Female Biased Sex Ratios Lead To Little or No Mate Guarding
A positive relationship between male-biased operational sex-ratios and copulation duration has been found in *A. uncinatus* [3]. Seasonal changes towards male biases in the operational sex ratio and copulation duration also support this prediction [3].

Prediction 5: The Higher the Density of Males, the Greater the Intensity of Mate Guarding
A correlation between male density and copulation duration, which supports this prediction, has been found in sympatric *Centrobolus* spp. [24]. In sympatric *C. inscriptus* / *C. annulatus*, the more common *C. inscriptus* also has a longer copulation duration [24].

Prediction 6: The Ease of Access by Rival Males to Mated Females Is Correlated With the Intensity of Mate Guarding
The mate-avoidance hypothesis and the pattern of mating by *C. inscriptus* provide support for this prediction because there is a difference between copulation durations on the ground compared to above ground [24]. The females in the trees would be more accessible than those on the ground.

Prediction 7: The More Costly the Defense of Mates In Terms Of Energy Expenditure, the Less Likely Males Are To Exhibit Mate Guarding
There is no direct test of this prediction in the Diplopods.

Prediction 8: The Greater the Risk of Injury While Mate Guarding, the Less Likely Males Are To Engage In the Behaviour
In the *C. inscriptus* mimic – *C. annulatus* models, the model is at greater risk from predation and has a shorter copulation duration which supports this prediction [24].

Prediction 9: The More Likely Males Are To Sacrifice Territorial Ownership While Mate Guarding, the Less Likely They Are To Exhibit High-Intensity Mate Guarding
This prediction could not be tested as millipedes are not territorial *per se*.

Prediction 10: The Longer the Interval between Copulation and Oviposition, the Less Likely Males Are To Remain In Association with Their Partners after Copulation
This prediction has not been tested in the Diplopods.

4. Conclusion
Evidence exists for all of Alcock's (1994) predictions of mate-guarding except for showing (1) mate guarding is energetically costly, and (2) as the time between copulation and oviposition protracts it becomes less likely for males to remain with their partners.

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