



OPEN Female *Phalangium opilio* use fellatio to compensate sexual avoidance

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Sexual conflict arises from differences in reproductive interests between the sexes. We allowed the female harvestman *Phalangium opilio* to sequentially mate with two different males to examine female sexual receptivity in this species. Virgin females were more sexually receptive than non-virgins. Males exhibited a high interest in repeated copulations with the same female, often engaging in aggressive behaviours such as biting and reversed sexual cannibalism. Fellatio, a behaviour in which females lick the male's penis, was observed in 44% of trials and was associated with female unwillingness to mate and shorter copulation duration. Fellatio was repeatable, suggesting that it is influenced by individual characteristics or underlying physiological factors. Female lifespan was negatively correlated with the total number of eggs produced, suggesting a trade-off between reproduction and longevity. These findings provide evidence of the appearance of fellatio, a female mating strategy that evolved as compensation of avoiding unwanted sexual intercourse.

Keywords Harvestman, Sexual conflict, Mating behaviour, Oral sex, Reversed sexual cannibalism, Female lifespan

Sexual conflict arises when the evolutionary interests of males and females diverge, leading to opposing selection pressures on reproductive traits and life histories^{1–3}. Males typically benefit from mating with as many partners as possible, as each mating provides an opportunity to sire offspring^{4,5}. In contrast, females do not require a high number of mates to maximize their reproductive output^{6,7}. Although females may gain some benefits from multiple mating, such as increased genetic diversity of offspring⁸, their fitness is usually maximized at an intermediate mating frequency^{9,10}. Beyond this optimal level, additional matings can become deleterious to females due to factors like risk of physical injury, increased time and energy expenditure, predation risk, risk of disease transmission and potential costs associated with male ejaculate components^{5,11–15}.

Resistance to mating can be costly for females. Male harassment behaviours like pushing, biting, chasing, forced copulations and genital mutilation can be risky and detrimental to female survival and reproductive success, even if the females are able to resist mating^{16–21}. Females can evolve resistance toward male harassment in the long term, but from the short-term perspective, female resistance can be costly, and sometimes fatal^{17,20,22,23}. These costs can be high enough that females may sometimes accept mating even when it is not their optimal strategy^{16,24}. For example, some female adzuki bean beetles (*Callosobruchus chinensis*) may accept mating even when it is not their optimal strategy, to avoid the higher costs associated with resisting male coercion⁷.

In this study, we investigate the behavioural evidence of sexual conflict in the common harvestman (*Phalangium opilio*). Reproductive biology of harvestmen is much less understood compared to spiders²⁵. During copulation, some females *P. opilio* displayed bouncing behaviour and attempted to flee, which is speculated to be a form of sexual conflict²⁶, similar to kicking harmful males in certain species^{7,27,28}. Alternatively, mating with an aggressive male may be an act of female choice for physically strong male²⁸ (Eberhard 2002), securing male offspring persistence traits from an aggressive father²⁹. In addition, males engage in penis rubbing on female mouth during precopulatory phase²⁶, but there were no attempts to experimentally address the functional significance of these behaviours.

Methods

Collection and maintenance

At the end of April 2024, approximately 230 subadult individuals of *P. opilio* were captured in Bratislava, Slovakia (48°5'56.47" N, 17° 6'8.43" E). Harvestmen were individually housed in plastic containers (diameter:

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7 cm, height: 7.5 cm) filled with wet cotton to maintain humidity and kept in a room at 24 °C and in a natural photoperiod. Ad libitum feeding with fish flakes, freshly sacrificed *Acheta domestica* and pieces of apple took place 2–3 times a week. The individuals used for the experiments were 10 to 15 days old. After experiments, cotton was replaced with moist coconut fibre, and plastic containers with females were transferred to a 26 °C climatizing chamber with 80% RH and a 12:12 h day/night regime. The number of eggs and the survival of females was checked every second day.

Mating behaviour

Individuals were weighed on an analytical balance to the nearest 0.0001 g, anaesthetized with CO₂, and the length of the prosoma was measured with digital callipers (to 0.01 mm). A female harvestman was randomly placed in a glass terrarium (30 × 20 × 20 [height] cm) lined with clean white paper. Willemart et al.²⁶ used similar terrariums, but the area available for locomotion in our experiment was three times greater. The male was immediately placed approximately 10 cm in front of the female. The time from the beginning of the experiment to the copulation duration (in seconds) of each copulation and the female resistance to the male mating attempt was recorded. Resistance was defined as the female's active rejection or escape of the male's mating attempts. Furthermore, we recorded occurrences of female active movements of chelicerae on male extruded penis and we defined this behaviour as fellatio (Suppl. video 1). The trial was terminated after 20 min by removing the original male. A new male was then placed inside the terrarium for an additional 20 min, and the same behaviour was recorded again. Each female was used twice, and each male was used only once.

Statistical analyses

Prosoma length and body mass did not differ between males used in the first and second round of mating trials ($t_{68} = 0.65$ and 1.46 , $P = 0.52$ and 0.15) and were not used in statistical analyses. Comparison of male and female biometry was performed with t-test for independent samples. Mating behaviour was analysed with Generalized Linear Mixed Model (GLMM), where the occurrence of copulation was defined as the binomial dependent variable. Female ID was defined as the random factor. Total number of fellatios or female resistances against males or summed copulation durations were continuous dependent variables with Poisson distribution. The predictors of female lifespan were examined with Cox regression.

Results

Morphological differences between sexes

The length and body mass significantly correlated in males, but not in females ($r = 0.32$, $P = 0.005$, $N = 74$ and $r = 0.00$, $P = 0.63$, $N = 39$, respectively). Male prosoma ($M = 1.05$ mm, $SE = 0.02$, $N = 76$) and body mass ($M = 0.03$ g, $SE = 0.000818$, $N = 76$) were significantly smaller than female prosoma ($M = 1.17$, $SE = 0.05$, $N = 39$) and mass ($M = 0.05$ g, $SE = 0.003$, $N = 39$) (t-test, $t = 4.19$ and 9.32 , $df = 113$, both $P < 0.001$, respectively).

Mating behaviour

Once the male was in physical contact with a female, the male quickly attempted to reach the head-to-head copulatory position. Intersexual interactions were extremely hostile; we recorded only 7/78 (9%) trials without apparent female resistance to aggressive males. The mean number of female resistance events was $M = 4.5$, $SE = 0.4$ ($N = 78$). Males always bite females on their legs and bodies. Four females were killed and partially cannibalized by males. Two of these females were killed during the first round after vigorous resistance to first (i.e., virgin) and second mating (i.e., non-virgin). The same scenario was observed for the remaining two non-virgin females; one copulated once and the second did not, but both resisted male sexual harassment. In one trial, the male broke the female's leg and in another trial the male lost one of his legs during an aggressive struggle. Virgin females were more sexually receptive than non-virgin females because copulations occurred significantly more frequently in the first round of mating trials (32/39) than in the second round of mating trials (21/37, two females cannibalized in the first round were removed) (GLMM, $\chi^2 = 5.45$, $df = 1$, $P = 0.02$). Female biometry was not a significant predictor of the occurrence of copulation (Suppl. Table 1).

Data from four cannibalized females were excluded from subsequent analyses. The latency to copulation increased significantly in the second round of trials. Males showed high interest in repeated copulations with the same female (up to 6 copulations per trial). The total copulation time was significantly longer in the first round than in second round of mating trials (GLMM, $\chi^2 = 36.72$, $df = 1$, $P < 0.001$, Table 1 & Suppl. Table 2). Fellatio occurred at least once in 31/70 (44%) of the mating trials and was performed by 23 of 35 females. It was observed predominantly after copulation (21/31, 68%). Females who used fellatio in the first trial were more likely to use it again in the second trial (12 females), and those that did not use it in the first trial were more likely to abstain from it in the second trial as well (14 females). Four females used fellatio only in the first round and five females used fellatio only in the second round. In other words, the probability of using fellatio in the second trial is significantly associated with its use in the first trial (Fisher exact test, $P = 0.007$). The more fellatios occurred in the trial, the shorter the total time the couple spent copulating (Fig. 1).

Fellatio was always associated with the downward position clearly indicating her unwillingness to mate. In this position, the male is unable to reach female's copulation chamber, and the female can engage the male's penis by licking. In particular, fellatio did not occur in the four cannibalistic trials. Females with larger body mass copulated for a significantly longer time (GLMM, $\chi^2 = 9.42$, $df = 1$, $P = 0.002$, Suppl. Table 2). Female resistance was positively and significantly associated with the duration of copulation (GLMM, $\chi^2 = 46.48$, $df = 1$, $P < 0.001$, Suppl. Table 2). When the number of all fellatios was defined as a dependent variable, fellatio was not influenced by female resistance, but positively by female mass and negatively by copulation duration (GLMM, $\chi^2 = 0.21$, 11.31 and 4.54 , $df = 1$, $P = 0.65$, < 0.001 and 0.033 , respectively, Suppl. Table 3).

	Round	Latency to copulation	Total number of copulations	Total copulation duration	All fellatios	All resistances
N	1st	30	35	35	35	35
	2nd	20	35	35	35	35
Mean	1st	3.93	1.8	91.7	0.943	4.23
	2nd	5.45	1.17	49.8	1.03	5.23
SE	1st	0.587	0.224	13.7	0.224	0.512
	2nd	1.11	0.241	9.45	0.261	0.687
Median	1st	3	2	76	0	4
	2nd	4	1	42	0	4
Minimum	1st	1	0	0	0	0
	2nd	1	0	0	0	0
Maximum	1st	14	5	354	5	11
	2nd	18	6	169	5	18

Table 1. Descriptive data of *P. opilio* mating behaviour.

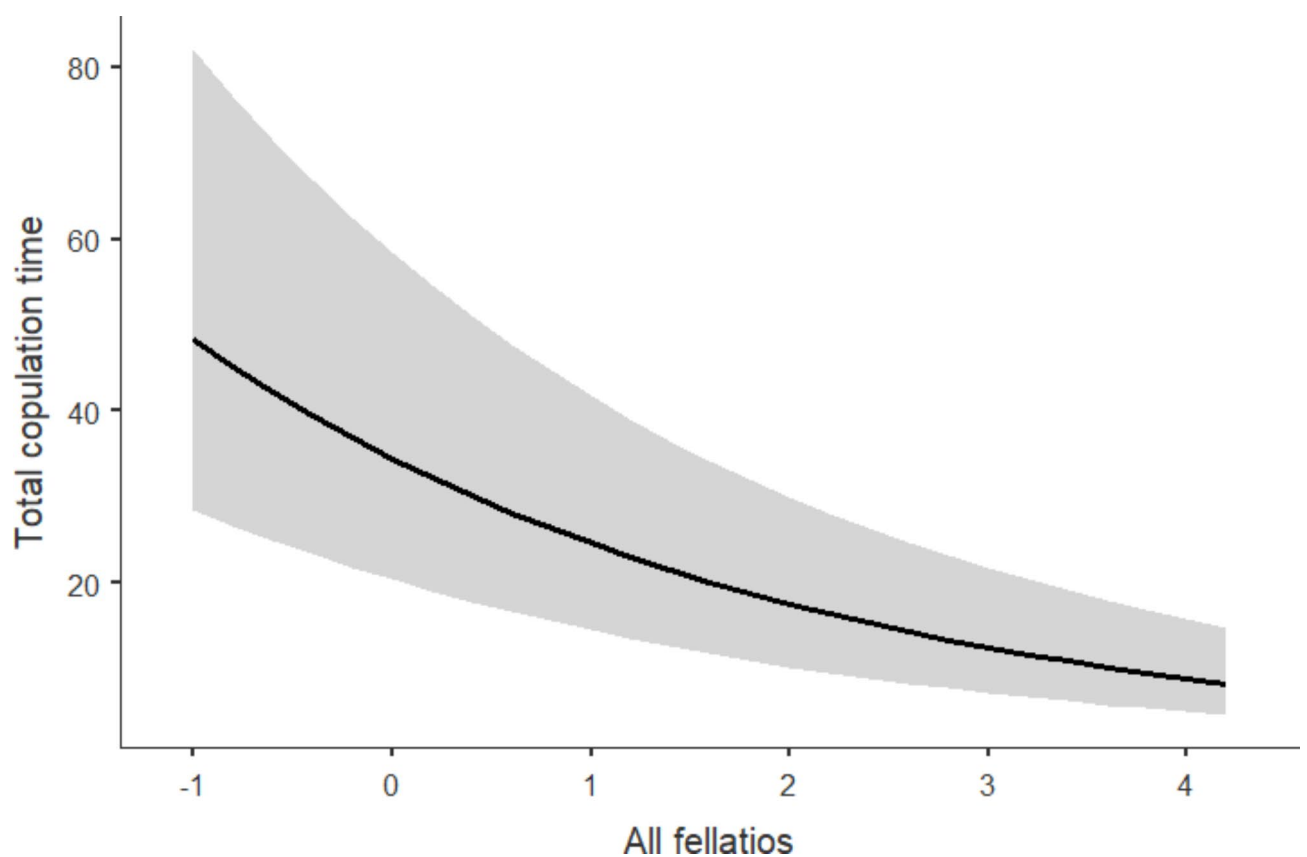


Fig. 1. Relationship between copulation duration and fellatio in *P. opilio*.

Reproductive success

Mean number of eggs was 30.54 (SE=8.85, range 0–196). After excluding 18 females who did not lay eggs, female fertility was positively and significantly influenced by female prosoma, negatively by female mass and negatively by fellatios (GLMM, $\chi^2=8.90$, 32.11 and 26.64, $P=0.003$, <0.001 and 0.001 , respectively, Suppl. Table 4). The removal of the female mass or the female prosoma from the model did not influence the direction of these relationships, suggesting that this was not an artefact of collinearity.

Female lifespan

The lifespan was negatively influenced by the total number of produced eggs. Other variables (total duration of copulation, prosomal length and mass, all resistances and fellatios) were not associated with female lifespan (Suppl. Table 5).

Discussion

Our research has shown that mating behaviour in the harvestman species *P. opilio* can be highly aggressive, with up to 10% of mating resulting in the death of the female. As far as we are aware, this is the first record of reversed sexual cannibalism in the order Opiliones. Female sexual receptivity apparently decreased after the first mating, and probably remate only when her sperm reserves become exhausted^{30,31}. *P. opilio* harvestmen do not rely on specific visual or chemical cues to locate sexual partners. They are unaware of each other's presence until physical contact occurs²⁶. This suggests that male-female interactions can be rare in the field and if physical contact happens, the male forcefully attempts to monopolize the female and copulate repeatedly. Biting the female's legs secures the male's contact with the escaping female.

Female choice is an alternative to the sexual conflict hypothesis^{28,29}. We suggest that (1) the risk of fatal injury by males, (2) lower propensity to remate, (3) longer latency time before copulation in the second round of trials, and (4) an extreme prevalence of female resistance across trials support the sexual conflict hypothesis rather than mate choice. Regarding the prevalence of female resistance, we suggest that resistant females would have more opportunities to escape aggressive males in the field than in constrained environment in the laboratory.

Females that produced more eggs had reduced lifespans compared to females with lower reproductive investment. It appears that heavily investing individuals are especially likely to incur long-term costs in terms of reduced lifespan as one of possible costs of mating^{32,33}. Interestingly, we did not detect any negative effect of mating on female lifespan^{11,15}.

Reversed sexual cannibalism is frequently interpreted as adaptive foraging^{34,35} and/or sexual size dimorphism³⁶. *P. opilio* females are somewhat heavier than males [26, this study], but males have larger pedipalps and chelicerae than females²⁶. Relatively larger males could be more dangerous for females during mating encounters. Unfortunately, we did not have enough events of males killing females for adequate statistical comparisons.

The occurrence of fellatio was inversely related to the total time the pair spent in copulation. Although fellatio has been documented in few non-human animals^{37,38}, our research for the first time showed that it can serve as compensation of female unwillingness to copulate. Moreover, this behaviour was repeatable, suggesting that the use of fellatio in harvestman females is a consistent behaviour that may be influenced by individual characteristics or underlying physiological factors. Interestingly, fellatio was not directly associated with behavioural evidence of female resistance toward hostile males, meaning that it evolved as an independent strategy how to avoid unwanted sexual encounters. More frequent fellatio negatively influenced female reproductive success. In our view, fellatio represents an expression of sexual conflict over remating, which incurs costs to females in terms of reduced reproduction. Specific physiological costs beyond the decrease in reproductive success require further research. We found that there was a positive relationship between the time females spend copulating with a male and the number of times they resist that same male's coercive mating attempts. While the possibility of females feeding on secretions produced in glands located in the male's penis cannot be ruled out²⁶, nuptial feeding would increase mating effort³⁹, which does not appear to be the case in *P. opilio*. It seems to be a result of sexual conflict over remating, where males evolve strategies to manipulate female mating interests, and females counter with resistance behaviour^{7,11,15}. The downward position of a female during fellatio indicates her unwillingness to mate and her control over that behaviour. As this coevolutionary process continues, males appear to be overcoming female resistance, potentially selecting for traits related to their ability to circumvent female defences. Other published evidence of precopulatory oral sex contact focuses on males stimulating females through cunnilingus^{40,41}, and this evolution does not seem to be compatible with the fellatio observed in *P. opilio*.

Limitations.

Firstly, our results are primarily empirical and lack direct experimental evidence. The potential functions of fellatio behaviour should be tested experimentally to prevent it (e.g., by glueing female chelicerae) and by comparing variables related to mating success and potential costs between groups with and without fellatio. Additionally, the costs of injuries on female reproductive success and lifespan should be assessed both experimentally and by comparing naturally injured and non-injured females.

Secondly, our experiments were conducted under laboratory conditions, which do not guarantee that harvestmen's behaviour is identical to that in natural conditions. It is possible that females in the field have more shelter and can avoid males during phases of low sexual receptivity. These issues need to be addressed in future research.

In conclusion, the mating system of the harvestman *P. opilio* appears to be heavily influenced by sexual conflict over remating. After their initial mating, females become less receptive to further copulations. In response, males attempt to mate with them forcefully and repeatedly. In addition to behavioural resistance against these coercive males, a significant proportion of females engage in a sexual strategy known as fellatio, which may serve to compensate for their sexual avoidance.

Data availability

All data used in the manuscript is available as supplementary document.

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Author contributions

P.P. designed the study, implemented the experiment and wrote the manuscript. P.P., J.L. and Z.P. performed the experiment.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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