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Male Morph Coexistence in the Bulb Mite Rhizoglyphus Robini – A Minor's Guide to Reproduction

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Summary to the thesis entitled:

Male morph coexistence in the bulb mite *Rhizoglyphus robini*

– A minor's guide to reproduction –

by Tom van den Beuken

In numerous animal species, alternative reproductive tactics (ARTs) can be found; these are discrete differences between members of one sex in terms of physiology, behaviour or morphology. Commonly two male types can be distinguished: 'majors' and 'minors'. Majors generally use precopulatory attributes to compete with rivals for copulations (i.e. weapons), or to favourably bias female choice (i.e. ornaments). These precopulatory attributes can be costly in terms of maintenance, locomotion (e.g. if they impede efficient locomotion) but also in terms of a survival e.g. if the precopulatory attributes makes the bearer more conspicuous to predators. Minors are unarmed and therefore do not have the costs of precopulatory attributes. Instead, some minors are thought to invest more resources in postcopulatory attributes, these are attributes that increase the chances of fertilizing ova during or after mating. Ample evidence exists of minors investing more than majors in postcopulatory attributes that help in sperm competitions. However, there are also postcopulatory attributes that can be used to increase female fecundity, and are thus useful outside of sperm competitions. For example, between-species comparisons have shown that males of species without precopulatory attributes transfer larger nuptial gifts (beneficial resources) than males of species with precopulatory attributes. However, to my knowledge, it is hitherto unknown whether there are also within-species correlations between precopulatory attributes and postcopulatory attributes that increase female fecundity.

To test if minors can invest more than majors in postcopulatory attributes that increase female fecundity, I used the male-dimorphic bulb mite (*Rhizoghlyphus robini*). Male bulb mites are either 'fighters' (eq. majors), which have a weaponized third leg pair, or 'scramblers' (eq. minors), which do not have weaponized legs. Using their weapons, fighters are able to kill rivals and, in small populations, monopolize females. Scramblers are unarmed and, contrary to some minors of other species, do not perform better in sperm competitions. Besides an earlier maturation time, scramblers have no clear fitness benefits. In chapter II, I showed that males that were fed for a single day after maturation sire more offspring than males that were starved from maturation onwards. I did not find differences in the reproductive output between the two-morphs. However, the differences between fed and starved males suggested that there may be a compound transferred from the male to the female that increases the number of eggs the female lays. Crucially, the production of this compound seemed limited by the male's energy budget. In chapter III, I built on this result and fed the mites for a more extended period of time. The result was that females mated to scramblers laid more eggs than females mated to fighters. This suggests that it is indeed possible for scramblers, or minors in general, to invest more than fighters (or majors) in postcopulatory attributes that function outside of sperm competition. Such a minor-specific benefit may play an important role in the maintenance of the male dimorphism in single populations.

Besides investments into postcopulatory attributes, a morph-specific level of intralocus sexual conflict (IASC) could also play a role in the maintenance of male dimorphisms. Males and females have different fitness optima for numerous traits, if these traits are regulated by the same genes in both sexes (for example body size) then this generates IASC where each sex tries to 'pull' the shared trait closer to its own phenotypic optimum. In turn, scramblers and fighters each have different trait optima, hence the level of IASC may differ between females and scramblers and between females and fighters. As a result of these morph-specific levels of IASC, life-history traits of offspring may be differently affected by paternal morphs. In chapter IV, I tested this by bidirectionally selecting for fighter or scrambler expression for several generations and comparing clutch composition and size, and life-history traits of the offspring between the two selection lines. I found that females from scrambler lines maintained a higher egg-laying rate and laid larger eggs (towards the final generations) than females from fighter lines. These findings could be the result of a more intense IASC between males and females in fighter lines than in scrambler lines. The benefits of mating with scramblers – or the costs of mating with fighters – for the offspring of females could affect female choice and, consequently, the maintenance of the dimorphism in single populations.

The killing of conspecifics by fighters has been a recurrent phenomenon in the experiments for this thesis, but by killing indiscriminately, fighter risk losing inclusive fitness. Inclusive fitness is the number of an individual's genes that it passes on itself plus the number of its genes that are passed on through relatives. Killers risk losing inclusive fitness if they kill (close) kin as they are then unable to pass on the killer's genes. Given the frequency of conspecific killing (e.g. chapter II), I hypothesized that there should be a selective benefit for killers that recognize kin and avoid killing them. In chapter V, I tested this hypothesis by making groups of fighters that were either brothers or unrelated, and assessed how many fighters per group were killed or cannibalised. I found that fighters tended to avoid killing and cannibalising kin, suggesting that there is kin selection in the bulb mite. Kin selection may therefore function as a means of avoiding inclusive fitness loss.

In a growing number of species, allometric scaling analyses in male-dimorphic species have revealed that these species are actually male trimorphic. In our bulb mite stock populations, we have observed that some unarmed males have an unusually bulbous body shape. Using allometric scaling, we found a breakpoint in the scaling relation between body length and leg width in unarmed males, evidencing that there is a third male morph: the 'mega-scrambler'. I hypothesized that the mega-scrambler is either a female mimic, a result of higher somatic buffering capabilities, or of an IASC that has moved farther towards the female trait optimum than the usual status quo.

In this thesis, I have demonstrated several potential fitness benefits of minor males in the bulb mite. To my knowledge for the first time, I have demonstrated that minor males may invest more resources than majors into postcopulatory attributes that allow them to sire more offspring outside of sperm competition. Secondly, I have shown that females in scrambler selection lines lay larger eggs and maintain a higher ovipositing rate for longer than females in fighter selection lines. Such fitness benefits may play an important role in the evolution and the maintenance of the male dimorphism. Besides these scrambler benefits, I have provided evidence for kin selection as I found that fighters tend to avoid killing and cannibalising kin more than non-kin. Finally, I provide evidence for a third male morph: the 'mega-scrambler'.