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〈Review〉

Male Mating Strategies through Manipulation of Female-perceived Predation Risk: A Minireview and a Hypothesis

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ABSTRACT: In this minireview we focus on how males may exploit female's sensitivity to predation risk in the context of mating. It has been shown in studies on guppies and jumping spiders that in response to altered female behaviors, which are adaptations to the unfavorable environment and a consequence of females' higher sensitivity to predator's presence as well as females' higher predation risk, males can adopt condition-dependent mating tactics. It appears that in such cases males do not modify their reproductive behavior directly in response to their own perception of predation risk, but indirectly in response to changes in female behavior induced by predator presence. It has also been recently shown in crabs that males can exploit female behavior by creating safer habitat spots, which increases the male mating success. Hence all the evidence suggests that males not only respond to female sensitivity to the natural variation in predation risk, but that males can also exploit female behavior by altering the environment. As a logical extension of these findings, we present a hypothesis that in certain conditions males can manipulate the environment in order to increase the predation risk and to induce female behaviors that enhance the male's mating success with the increased predation risk. We propose that such a manipulation to increase predation risk is expected to evolve in males of species with a strong sexual conflict and female-biased predation risk. Although empirical evidence has not been yet shown, initial observations in a water strider species in Korea, *Gerris gracilicornis*, seem to support this hypothesis.

Key words: *Gerris gracilicornis*, Manipulation, Predation risk, Sensory exploitation, Water strider

INTRODUCTION

Predation risk influences reproductive behaviors, such as mating activity or mate choice (Gwynne 1989, Lima and Dill 1990, Sih et al. 1990, Magnhagen 1991, Sih and Krupa 1995). Predation risk can operate as a cost or a benefit (Gwynne 1989, Hedrick and Dill 1993). Although in some species males or females may experience reduced predation risk during mating (e.g. due to chemical defense against predators as in the stick insect *Diapheromera veliei*; Sivibski 1980; or due to confusing effect of pheromones as in the red-spotted newt *Notophthalmus viridescens*; Verrell 1985), in most species predation risk imposes higher cost of reproduction (Lima and Dill 1990, Magnhagen 1991, Pocklington and Dill 1995). Higher mortality of mating pairs may be caused by reduced mobility and a higher conspicuousness of a mating pair (Gwynne 1989). If an individual ignores presence of predators, it could be captured, which clearly leads to a decrease in its fitness. Therefore one expects that individuals should be sensitive to predation risk in the context of reproductive behaviors.

Although predation risk as a cost of reproduction has received increased attention, the research focused on male's perspective. Many studies of sexual selection have shown an increased risk of predation due to the presence of male's ornaments (Andersson 1994). Elaborate and visually conspicuous ornaments and displays of males can attract predators as well as females. In addition to using vision, predators can perceive prey's location by cuing on mating signals in a variety of modalities, including acoustic and chemical signals. Mediterranean house geckos can approach calling of male crickets (Sakaluk and Belwood 1984). In contrast, less attention has been paid to the effects of predation risk on mating behavior from the female's perspective, and female behavior has been largely ignored as an important selective force (Rosenqvist and Berglund 1992). Females may suffer higher predation risk and they may be more sensitive than males to the predator presence. For example, in the Túngara Frog *Physalaemus pustulosus* response patterns to an increased predation risk differ between sexes (Bernal et al. 2007). Bernal et al. (2007) showed that male Túngara Frogs increased his mating calls even in highly risky environments provided that male perceives other competitor male's calls. In contrast, female Túngara frogs *Physalaemus pustulosus* were not attracted to male's mating call when predation risk was high (Bernal et al.

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2005). Hence, males, unlike females, were trying not to lose opportunity for reproduction in spite of increased predation risk. Here we review recent evidence that: (*a*) males in some species appear to use such predator-induced changes in female behavior to adjust their own (the male's) mating tactic, and that (*b*) the males appear to create situations of lower predation risk in order to exploit female behavior so as to increase the male's mating frequency. Furthermore, a hypothesis is proposed that in certain conditions males, who are less sensitive to predators or suffer lower predation risk than females, may manipulate an environment to increase the perceived predation risk in order to coerce a female to mate. We hypothesize that a male may create a situation where a female has to choose between accepting the mating (and benefiting the male's fitness) or experiencing an increased predation risk.

FEMALE-BIASED PREDATION RISK: FACTORS LEADING to INCREASED FEMALE'S PREDATION RISK

Although males are often regarded as the sex who suffers higher predation risk due to the conspicuous traits, there are situations in which the predation risk of females is higher than that of males. When females mate-search or choose their mates, their risk of predation may increase. Choosing mate or mate searching activity is costly behavior. Hedrick and Dill (1993) showed that female crickets, *Gryllus integer*, experience enhanced predation risk because they are attracted to conspicuously calling males that attract attention of predators. Male *G. integer* attracts females with a rapid trill. Females move towards calling males, often across open habitats, which makes them vulnerable to visually-hunting predators. In addition, female sand gobies *Pomatoschistus minutus*, a marine fish common on the coasts of Europe, spend a lot of time searching for mates. Mate searching activity is dangerous because it increases the probability of encountering potential predators.

Without predators, females prefer large and bright males. But females lose their choosiness when predators exist (Forsgren 1992). Second, the female's typically larger body size makes them more profitable prey that is more easily captured. Female guppies *Poecilia reticulata* suffer higher predation risk than male guppies (Pocklington and Dill 1995). Because male guppy has bright spots in his body, it had been generally expected that elaborate males suffer higher predation risk than females. But Pocklington and Dill concluded that larger female body caused female-biased predation risk. Moreover, Su and Li (2006) also showed that larger female jumping spider, *Jacksonoides queenslandicus*, is the more profitable prey for predatory jumping spider *Portia fimbriata*. In mammals, females of the small desert rodent *Peromyscus maniculatus*, were more vulnerable to their avian predator, the great horned owl *Bubo virginianus* (Longland and Jenkins 1987). As great horned owls preferred larger prey, and variance of body mass of females is larger than body mass of males, large females were at the highest predation risk

When a female is gravid or pregnant, her ability to escape is lowered. Especially, in viviparous animals, pregnancy is associated with lower locomotor performance. Gravid garter snakes, *Thamnophis elegans*, spend a lot of time basking (Seigel et al. 1987). Such reduced locomotor performance leads to an increased predation risk. Also, gravid Scincid lizard *Leiolopisma coventryi* females have lower running speed, which probably leads to increased predation by white lipped snakes *Drysdalia coronoides* (Shine 1980). In a copepod *Cyclops vicinus* egg carrying also leads to higher predation (by sticklebacks; Vuorinen et al. 1983). In addition to a decreased escaping ability, gravid female prawn *Palaemon adspesus* suffered increased vulnerability to predator fishes due to highly conspicuous colorful eggs visible through their bodies (Berglund and Rosenqvist 1986).. Finally, if females carry their offspring on their backs, such as in the common striped scorpion *Centruroides vittatus*, their pre-

Table 1. Examples of causes factors leading to increased female's predation risk

Cause	Species	Reference
Being attracted to male's signal	Crickets *Gryllus integer*	Hedrick and Dill 1993
	Gobiid fish *Pomatoschistus minutus*	Forsgen 1992
Large body size	Guppy *Poecilia reticulate*	Pocklington and Dill 1995
	Jumping Spider *Jacksonoides queenslandicus*	Su and Li 2006
	Deer mice *Peromyscus maniculatus*	Longland and Jenkins 1987
Pregnancy	Common striped scorpion *Centruroides vittatus*	Shaffer and Formanowicz 1996
	Prawn *Palaemon adspesus*	Berglund and Rosenqvist 1986
	Garter snakes *Thamnophis elegans*	Seigel et al. 1987
	Scincid lizard *Leiolopisma coventryi*	Shine 1980
	Copepod *Cyclops vicinus*	Vuorinen et al. 1983

dation risk is higher then that of females carrying eggs. Female scorpions with young instars on their backs, suffer a decreasing running speed (Shaffer and Formanowicz 1996) which may increase their vulnerability to predators.

HIGHER SENSITIVITY OF FEMALES TO PREDATORS: EXAMPLES OF PREDATOR-INDUCED BEHAVIORS

Female mating behavior can be changed under the risk of predation. Predation risk of females may be increased or be higher than the predation risk of males ("female-biased predation risk") due to the causes we mentioned above. Additionally, females can be more sensitive to predators than males even in male-biased predation risk due to female high reproductive value. Thus females may develop higher sensitivity and more elaborate behaviors to avoid predators (Table 2).

First, females prefer safer micro-habitats. Koga et al. (1998) showed that female fiddler crabs *Uca beebei* decreased mate-searching activity when predator birds are present. As crabs were attracted to objects to hide, female crabs may prefer male courtship structures that guarantee more safety during mate searching (Christy 1995). Indeed, the preference of female *U. terpsichores* crabs for males with hoods increases with predation risk because hoods can offer a refuge from predators (Kim et al. 2007). Water strider *Gerris buenoi* females also preferred the habitat with abundant refuge (Rowe 1994). Without the refuges, female water striders were more vulnerable to predators than males (Arnqvist 1989, Rowe 1994). Also, in high-risk environment, female Túngara frogs *Physalaemus pustulosus* were not attracted to male's mating call and stayed in safe microhabitats (Bernal et al. 2007).

Second, a female can restrict her general mobility in response to predators. Cooper et al. (1990) showed that gravid female lizard *Eumeces laticeps* became less active, and relied on crypsis rather than on running away (running speed of gravid female is slower). This tendency is also shown in another lizard species. Antipredatory defenses of gravid female southern water skinks *Eulamprus tympanum* also rely on crypsis, rather than on rapid escape from birds or snakes (Schwarzkopf and Shine 1992). The decreased agility of gravid female skinks did not lead to increased predation risk, but it allowed avoiding predation through lower conspicuousness resulting from lower mobility (Schwarzkopf and Shine 1992).

Third, females may become less choosy in mating interactions when predators are present. As we mentioned earlier, Hedrick and Dill (1993) showed that female cricket *G. integer* became less choosy because traveling to calling male increases predation risk. For the same reason, as predation risk increases, female sand goby accepts smaller, duller males (Forsgren 1992). Also female guppy became unreceptive or less selective (Gong and Gibson 1996) and accepted forceful mating (or sneaky mating) by males (Magurran and Nowak 1991) in higher predation risk treatments. In the case of green swordtails *Xiphophorus helleri*, female's preference for elaborate males disappeared in the presence of predatory cichlids (Johnson and Basolo 2003).

Finally, females may avoid copulation if predation risk is high. After the sunset, a flightless female firefly *Photinus collustrans*, leaves her burrow and sends flash responses to male's signals. These flashes may, however, attract predators. Therefore, in the risky environment, females reduced the time of being outside the burrow for mating (Wing 1988). Copulation duration of this species was relatively shorter than in other species', which seemed to be related

Table 2. Examples of anti-predatory adaptations of females

Activity	Species	Reference
Safer habitat	Fiddler crab *Uca beebei*	Koga et al. 1998
	Fiddler crab *Uca terpsichores*	Kim et al. 2007
	Water strider *Gerris buenoi*	Rowe 1994, Arnqvist 1989
	Túngara frogs *Physalaemus pustulosus*	Bernal et al. 2007
Decreased mobility	Lizard *Eumeces laticeps*	Cooper et al. 1990
	Water skinks *Eulamprus tympanum*	Schwarzkopf and Shine 1992
Less choosy	Cricket *Gryllus integer*	Hedrick and Dill 1993
	Gobiid fish *Pomatoschistus minutus*	Forsgren 1992
	Guppy *Poecilia reticulata*	Magurran and Nowak 1991, Gong and Gibson 1996
	Green swordtails *Xiphophorus helleri*	Johnson and Basolo 2003
Avoid copulation	Firefly *Photinus collustrans*	Wing 1985, 1988
	Cyclopoid copepod *Cyclops vicinus*	Maier et al. 2000
	Bank voles *Clethrionomys glareolus*	Ronkainen and Ylonen 1994

to an increased selective pressure by predators (Wing 1985). Also, the cyclopoid copepod *Cyclops vicinus* avoided mating and decreased activity when a predator fish was present because mating pairs or egg-bearing females were more vulnerable to attacks by predators than virgin females (Maier et al. 2000). Similarly, female mating behavior of bank voles *Clethrionomys glareolus* was suppressed by the threat of mustelid predators: Ronkainen and Ylonen (1994) showed female voles avoided copulation after sensing the odor of predators, but males did not change their mate searching behavior under the predation risk.

MALE RESPONSES TO FEMALE'S PREDATOR-INDUCED BEHAVIORS - EXAMPLES

Previous studies have interpreted modified behaviors of prey under the risky environment from the male-biased perspective because actively mate-searching males can be exposed to predators. If the reproductive benefit from copulating with more mates and from actively searching for females is higher than the survival cost, males would be less sensitive to predation risk. In contrast, females, who prioritize the reproductive value, may behave unlike males and may be more sensitive to predation risk under the same risky environment. Subsequently, males may alter their behavior in response to modified behavior of females. In such a situation the behavior of both sexes may be apparently changed by the predation risk, but only the behavior of females would be in the direct response to predation risk, while the behavior of males would be affected by predators only secondarily.

Under elevated predation risk, male guppies switch from courtship display to coercive mating attempts (Magurran and Nowak 1991). Previously it had been known that male guppies change their own mating tactic after directly perceiving predation risk. However, recently, it was shown that transition of males' mating tactic is caused by predator-induced changes in female behavior (Evans et al. 2002). Female behavior under predation risk increases the relative efficiency of male coercive mating attempts because females become less choosy under predation risk. Consequently, males adaptively shift their behavior by switching to coercive mating. The most important conclusion is that this change in male behavior is not directly induced by the predator, but indirectly by the changes in female behavior.

Jumping spider *J. queenslandicus*, which we mentioned above as an example of species with female-biased predation risk, also showed changes in male behavior in response to predator-induced changes in female behavior. When only females jumping spiders were exposed to predatory jumping spider *P. fimbriata*, conspicuous leg-flicking display duration of males decreased (Su and Li 2006). However, when only males were exposed to the predator, the display duration was not significantly different from the duration in no-predator situation (Su and Li 2006). Therefore, similar to guppy's case, male jumping spider's courtship behavior is not influenced by predation risk directly, but by predator-induced alteration in female behavior.

MALES EXPLOIT FEMALE BEHAVIOR BY CREATING SAFER ENVIRONMENT: RECENT DISCOVERIES

Both, guppy and jumping spider studies showed that males adaptively respond to female behavioral shifts induced by increased predation risk. However males appear to be able to alter the environment and exploit female's preference so that the male mating success is increased. For example male fiddler crabs *Uca terpsichores* exploit female's preferences by building a hood structure as a safer habitat under the high risk of predation (Kim et al. 2007). Structures, such as hoods, semi-domes, domes and pillars, are built at the entrance of their burrow by reproductive males of 18 of the 97 species in the fiddler crab genus *Uca* (Christy et al. 2002). More structures are constructed when females were presented (Kim et al. 2004) and they could be used as a refuge under high predation risk (Kim et al. 2007). Therefore, exploiting female's sensory preference for safer structures in a risky environment, the male crabs lure the females into his hoods for mating (Kim et al. 2007). Male fiddler crabs (genus *Uca*) suffer high predation risk than females due to their enlarged, bright colored claws (Koga et al. 2001) and males can be more vulnerable when attracting potential mates outside their burrows. However, if structures of the male fiddler crab enhance his mating success, provide females with direct survival benefits, and offset the cost of decreased survival of males under the high risk of predation, the sensory exploitation of females by males might have evolved.

MALES MANIPULATE FEMALE MATING BEHAVIOR WITH INCREASED FEMALE-PERCEIVED PREDATION RISK BY CREATING MORE RISKY ENVIRONMENT: A HYPOTHESIS

We suggest that in some species, males manipulate female mating behavior by increasing female-perceived predation risk. Based on our initial observations of waterstriders, we suggest that male water striders can benefit by making females more at risk. Rowe (1994) showed that mating female water striders *Gerris buenoi* suffers higher predation risk than male in mating. Female insects on land can survive attacks by predators due to the position in mating: the female is less vulnerable when male is on the top of female in mating. In contrast, in aquatic insects, the situations of two sexes may be reversed. If predators attack the aquatic insect in the water or along the water surface, the female under the male will be more vulnerable. Generally male water strider mounts on the top of a female. Because male is on the female in mating, predator, such as backswimmers, frogs, and fishes, that approaches in the water or along the water surface can attack female at first. Therefore female water striders are expected to be more sensitive to predators' presence. If females are indeed especially sensitive to predators' presence, male water striders may manipulate female mating behavior by affecting the female-biased predation risk so as to enhance the male's mating success.

Our initial observations suggest that male *G. gracilicornis* seems to use this kind of mating strategy: by producing conspicuous vibrations on the water surface at the very initial phase of mating on the top of the mating female, males appear to increase female-biased predation risk (Han et al. 2007). As the predators are sensitive to the ripple signals, which may contain information on the location of the prey, they may be attracted by precopulatory signals of male *G. gracilicornis*. Male is expected to suffer less from attracting additional predators due to the mating position as described above. Out initial observations suggest that males stop producing signals right after the mating female extends her genitalia. Females that do not extend their genitalia may suffer increased predation risk due attraction of predators to the mating pair. The extensively documented conflict between sexes over the mating frequency and duration in waterstriders (Arnqvist and Rowe 2005) selects for female's opposition to mating. Thus, the hypothesis proposes a new strategy by males to "win" the evolutionary conflict between sexes: the male coerces female to copulate by increasing the predation risk as long as the female does not allow for a copulation to start. In response to sexually antagonistic coevolution, behaviors or morphological characteristics of the male to overcome female resistance would be favored (Arnqvist and Rowe 2002a, 2002b). Consequently, we propose that the precopulatory signals of *G. gracilicornis* are used for overcoming female resistance and inducing the initiation of copulation quickly.

According to the above hypothesis, mating males *G. gracilicornis* attract predators and make the environment riskier to females and, consequently, manipulate female mating behavior for enhancing the males' mating success by exploiting female's sensory preferences. In contrast, the male fiddler crabs in Kim's (2007) study do not manipulate the predators' behavior, but only create safer spots within the risky environment in order to exploit female's sensory preferences for staying in, or running towards, these safer microhabitats (Fig. 1). When the unfavorable environment for females is formed by the waterstrider male, who is relatively less influenced by such unfavorable environment, the male benefits from manipulating females by exploiting females' higher sensitivity to predation risk in this unfavorable environment (Fig. 1). This hypothetical mechanism is based on a premise that males are little affected by attracting the predators.

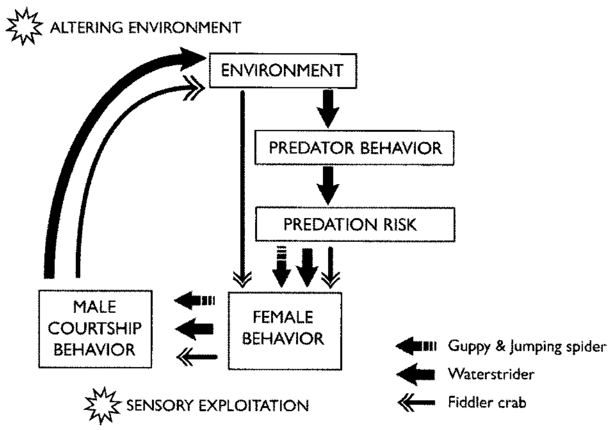

Fig. 1. The mechanism of manipulating female behaviors.

CONCLUSION

This paper suggests that, when both sexes are under the strong sexual conflict about the reproductive interest, males can exploit the sensory system of females and manipulate behavior of females for increasing their own mating success when females are more sensitive to the potential predators. Previous studies have indicated that males are disadvantageous under the predation risk due to their elaborate display. However, the typically cryptic females can often experience higher predation risk then males. It is argued that in this situation, males can adopt behaviors that increase predation risk of the female and consequently manipulate female behavior so that the male mating success is increased. This subject has been largely ignored and we hope that this brief review offers perspective for the future studies in this area.

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