

Mating rock shrimp hedge their bets: old males take greater risk, but only after careful assessment of the investment scenario

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Abstract Mature organisms often have to trade reproductive opportunities against the need to survive, especially in species with exaggerated, sexually selected traits. Life history theory predicts that old males with low residual reproductive value (RRV) would accept greater risk for current reproduction than their younger counterparts. Accordingly, we tested the prediction that, under predation risk, old males of the rock shrimp *Rhynchocinetes typus* pair with females faster and for a longer time than young males do. We exposed young and old dominant males (in the final ontogenetic stage, called “robustus”) to a female in the absence and presence of a predator. As predicted, older robustus males modified their mating behavior when exposed to a predator. However, in contrast to the prediction, they delayed female seizure under predation risk, possibly to carefully assess the actual threat before initiating female guarding. Once they had established the mate-guarding position, old robustus males did not interrupt it until the end of female spawning and, in the presence of predators,

even guarded the female significantly longer than in predator-free treatments. In contrast, younger robustus males did not delay female seizure but abandoned the female repeatedly when a predator was present, suggesting that they perceived and responded to the predation risk. Our results suggest that older robustus males have the experience to assess threats before engaging in risky behaviors that bolster their reproductive success. Although consistent with the theory that low RRV individuals should accept greater reproductive risk, we suggest that old individuals do not recklessly engage in risky behaviors but rather cautiously evaluate the threats before investing in a potentially terminal reproductive event.

Keywords Age · Mate-guarding · Mating behavior · Predation risk · Residual reproductive value · Risk-taking strategies

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Introduction

To maximize fitness, adult organisms must balance the opportunity for reproduction against the likelihood of survival (Lima and Dill 1990; Magnhagen 1991; Andersson 1994). Sexually selected behavioral and morphological traits, commonly more developed in fully mature individuals, not only generate greater energetic costs but may also cause high predation risk (e.g., Kotiaho et al. 1998; Zuk and Kolluru 1998; Koga et al. 2001; Cordes et al. 2014). The risk taken during reproduction may depend on traits intrinsic to an individual, such as age (e.g., Pianka and Parker 1975; Clutton-Brock 1984; Part et al. 1992; Fischer et al. 2008), and external factors, such as predation (e.g., Lima 1998a; Borowski 2002; Christy 2007). The effects of both predation and age on risk taking during mating have been well documented, but their interactive effects are still poorly understood, even though

they could have important consequences for the fitness of individuals and the population dynamics of a species.

Life history theory predicts that an individual should adjust its reproductive effort as its residual reproductive value (RRV, sensu Williams 1966), i.e., the expectation of future reproduction, decreases with age (Williams 1966; Pianka and Parker 1975). Old individuals (with low RRV) should be willing to accept greater risk in current reproduction than younger conspecifics should, which, if killed, jeopardize an entire lifespan of reproduction (as outlined in the “terminal investment” hypothesis; Pianka and Parker 1975; Clutton-Brock 1984). Indeed, in the presence of predators, old males of various species take greater risk than do young males (e.g., fish *Gobius niger*: Magnhagen 1990; collared flycatcher *Ficedula albicollis*: Part et al. 1992; three-spined stickleback *Gasterosteus aculeatus*: Candolin 1998; butterfly *Hypolimnas bolina*: Kemp 2002; moth *Achroia grisella*: Lafaille et al. 2010). However, there is also some indication that, in general, young individuals (with high RRV) invest more in current reproduction than do older males when they are poorer competitors (e.g., Billing et al. 2007; Engqvist et al. 2015) or in better nutritional condition (Hunt et al. 2004; Wilgers and Hebets 2012). Age may have contrasting effects on different components (e.g., fighting ability, egg production) of reproductive effort (Kemp 2006; Trumbo 2012), reflecting individual variation in the cost-versus-benefit of engaging in specific mating behaviors (see Cooper 1999; Kemp 2002).

Mating events usually comprise a pre-copulatory (mate search, mate assessment, and courtship) and a copulatory phase (pair guarding and fertilization), during which reproductive effort (e.g., accepting predation risk) may differ depending on the intensity of behavioral activities (e.g., Trumbo 2009). Under predation risk, males often behave more cautiously and reduce the intensity of conspicuous courting behaviors (Candolin 1998; Koga et al. 1998; Lima 1998b) which commonly results in fewer or delayed pairings (e.g., Lasley-Rasher and Yen 2012). In some species, males abandon conspicuous courtship and directly engage in brief sneak matings (Magurran and Seghers 1990; Godin 1995). In mate-guarding amphipods, the threat of a predator led to a reduced overall activity of most males, resulting in lower proportion of pair formation (Dunn et al. 2008). However, males that paired under predation risk became less discriminant in the choice of their sexual partner and formed mate-guarding pairs faster than did males under no risk (Mathis and Hoback 1997; Dunn et al. 2008), implying a trade-off between reproductive success and survival. As these studies did not take into account potential differences in RRV among males, it is possible that mating males that accepted high risk might have had lower RRV.

In polyandrous species, male reproductive success is mostly determined during the copulatory phase (Arnqvist and Danielsson 1999; Turnell and Shaw 2015), and thus,

differences in risk taking between young and old males should be most pronounced in this phase. During the copulatory phase, mates often shorten pair guarding under predation risk, regardless of whether overall guarding is long (days, Hartnoll and Smith 1978; Dunn et al. 2008) or short (hours, Wilber 1989; Sih et al. 1990). Guarding of females is risky for males; they may be more detectable (Verrell 1985; Maier et al. 2000) or have impaired escape responses from predators (review in Jormalainen 1998; Zeiss et al. 1999). Consequently, males with high RRV may shorten the duration of female mate guarding. On the other hand, pair guarding can enhance female survival (Wilber 1989; Rodríguez-Muñoz et al. 2011) or improve fertilization success, thereby leading to overall greater reproductive success. Thus, once they have copulated with the female, the investment of old males should increase under predation risk in order to guarantee the success of one of their final mating efforts. It can be hypothesized that old males accept greater risk and guard females for longer time periods than young males do.

Based on the above considerations, we tested the general hypothesis that old males invest more in current reproduction than do young males by taking more risk in the face of perceived predation. We used the rock shrimp *Rhynchocinetes typus* as model organism; predation risk may especially affect the costs of reproduction in species with complex mating behavior such as rhynchocinetid shrimps (Correa and Thiel 2003a). At maturity, *R. typus* males go through different ontogenetic stages: males become sexually mature in the “typus” stage (morphologically similar to females) and then pass through several intermediate stages (named “intermedius”) before reaching the terminal moult stage which is termed “robustus” (Correa et al. 2000). Males stay in the robustus stage for several months (P Bravo, personal communication), during which they concentrate the highest reproductive potential (see Hinojosa and Thiel 2003) and potentially achieve the majority of their reproductive success (see Bailie et al. 2014). As the final moulting stage, robustus males progressively accumulate epibionts and parasites on their carapace and cannot renew appendages (e.g., chelipeds, maxillipeds, eyes) damaged during fights with other males (see Thiel et al. 2010 for *Rhynchocinetes brucei*), thereby likely reducing their survival and fighting ability (i.e., Resource Holding Power; sensu Parker 1974). As survival is thought to decline and reproductive success supposed not to increase with age, it is safe to assume that old robustus males have lower RRV than their younger counterparts have.

In this study, we investigated whether dominant *R. typus* males exhibited age-specific behavioral differences during pre-copulatory and copulatory phases under differential predation risk. We tested the specific hypotheses that old robustus males take greater risk by rapidly seizing females and guarding them for longer than young robustus males do.

Materials and methods

Study species

Rhynchocinetes typus is common on rocky reefs along the Peruvian and Chilean coasts (Miranda and Kong 1970), where they are prey for many fish species (Vargas et al. 1999; Medina et al. 2004; Ory et al. 2012). Robustus males are dominant over males of other stages; they possess highly developed chelipeds (first pereopods) and third maxillipeds, which they use during courtship and intrasexual competitive interactions (Correa et al. 2003). Copulatory pairs are formed when a male seizes the female and encloses her with its pereopods, third maxillipeds, and abdomen in the so-called cage state (sensu Correa et al. 2000, see also Fig. S1a, b). Initially, the male engages in stimulatory behaviors before starting to transfer several spermatophores (Correa et al. 2000). Shortly after transfer of the first spermatophore, the female initiates spawning (Thiel and Hinojosa 2003). Robustus males guard the female for several minutes to a few hours throughout the entire spawning process, before releasing it (liberation). The time between female first spawning and liberation is called “reproductive cage”; it refers to robustus male efforts to ensure egg fertilization.

Shrimp and fish collection and maintenance

Shrimps were collected from shallow subtidal hard bottoms waters in Bahía La Herradura, Coquimbo, Chile (29° 59' S, 71° 22' W), with an airlift sampling device (see Correa and Thiel 2003b) and baited traps. In the laboratory, shrimps were sorted into old robustus males, young robustus males, other males, and females. These four categories of shrimps were kept in four separate tanks (L×W×H=50×40×20 cm) under a natural light regime, with aerated running seawater pumped from 4 m depth in La Herradura bay nearby.

Old robustus males are easily distinguished from younger robustus males by their darker exoskeleton and dactylus hairs and the epibionts, such as the polychaete *Romanchella pustulata* (Serpulidae), that accumulate on their carapace. Robustus males that could not be clearly categorized as either young or old according to these three criteria were not used in the experiments. All shrimps were fed ad libitum with tunicates *Pyura chilensis* (Pyuridae).

The female tanks were checked daily for exoskeletons which indicate that a female had moulted recently. These newly moulted females can be distinguished from non-receptive females based on their lighter coloration and soft exoskeleton; they were isolated for 12–36 h before being used in the mating experiments (see below). A robustus male (not used in the mating experiment) was then placed with the female which was considered receptive if seized by the male; a female thus confirmed to be receptive was then immediately used in the mating experiments (see below).

The labrisomid *Auchenionchus microcirrhys*, a common predator of decapod crustaceans in Chilean waters (Muñoz and Ojeda 1997, see also van Son and Thiel 2006), was used as predator in the experiments. A single fish individual (25 cm total length) had been captured in La Herradura bay using a gill net and was kept in the seawater laboratory for approximately 2 months, until it was well acclimated to laboratory conditions. For the shrimp experiments, this fish was further acclimated in a (200×70×60 cm) tank with running seawater for ~2 weeks before being used for the experiments. The fish was fed once a day with dead or live *R. typus*, and it behaved apparently normal, rapidly consuming the offered rock shrimps. Furthermore, potential artifacts from atypical behaviors of the fish would have likely been similar among all treatments, thus allowing comparison of young and old robustus male-mating behaviors.

Experimental setup

The effects of predation risk (predator absence vs. presence) and shrimp age (young vs. old) on the duration of *R. typus* mating behaviors (see below) were tested using a factorial 2×2 balanced and orthogonal experimental design with six replicates per treatment combination (total number of trials=24). Experiments were conducted in two large transparent glass tanks (140×65×26 cm) filled with 20 cm seawater. A small tank (50×40×20 cm) filled to the top with seawater was placed in the center of each large tank. Two days before a trial, a robustus male, five typus males, and five non-receptive females were placed in the small experimental tank with aerated running seawater to acclimatize and were fed daily with tunicates. This 1:5:5 ratio was similar to that observed in natural *R. typus* populations (Correa and Thiel 2003b). The typus males were used in the experiment because, in the field, they are usually the first to locate a receptive female with which they start mating, thereby creating visual cues that are used by robustus males to locate the females (Diaz and Thiel 2004; Thiel and Correa 2004). The non-receptive females were added to obtain a sexual ratio in the experiments that is similar to that of natural populations. Typus males and non-receptive females were marked with small (5 mm in diameter) colored plastic tags glued to their cephalothorax with a fast-setting cyanoacrylate glue. Preliminary observations found no effects of tags on shrimp activity. A small rock was placed in each of the four corners of the tank to provide refuges to the shrimps.

Ten minutes before the beginning of a trial, a receptive female (referred hereafter as “female”) was placed under a transparent plastic bell in the small tank with the other shrimps to acclimatize. Just after the receptive female was placed under the transparent bell, the predatory fish *A. microcirrhys* was released in the large, outer tank with no access to the shrimps inside the small tank. A trial started when the plastic bell was removed, allowing the female to move freely and interact with the other shrimps inside the tank.

All shrimps were used only once during the experiment. In total, 12 young (carapace length 20.0 ± 1.2 mm, mean ± 95 % confidence intervals) and 12 old (19.0 ± 1.1 mm) unique robustus individuals of similar size ($t=1.29$, $P=0.21$, $df=22$) were used as focal males. Twenty-four unique females (13.5 ± 0.7 mm) were used as receptive females. A new set of five typus males (120 individuals in total) and five non-receptive females (120 individuals in total) were used for each trial.

Shrimp behaviors

During each trial, five shrimp behaviors, typically observed during *R. typus* mating (Correa et al. 2000), were recorded (Table 1 and Fig. 1a): first contact of robustus with the female, seizure of the female by the robustus male (i.e., beginning of pair guarding), female spawning, transfer of spermatophores by the robustus male to the female, and liberation of the female by the robustus male (i.e., end of the reproductive cage; see also Fig. 1a). The number of spermatophores that robustus males transferred to the female was also counted but was not included as a variable in the analysis to avoid collinearity (Quinn 2002) because it was highly correlated to the duration of the spermatophore transfer phase (Spearman $\rho=0.52$, $P<0.01$). The time of occurrence of each behavior was recorded and used to calculate the duration (min) of five reproductive phases important for the *R. typus* mating success (van Son and Thiel 2006): pre-contact, pre-seizure, pre-spawning, reproductive cage duration, and spermatophore transfer phases (see Table 1 and Fig. 1a for the description of the different phases).

Table 1 Male and female behaviours of which time of occurrence (min from female release) was recorded during the experiments. Reproductive phases (dependent variables used in the analysis) of which duration (min) equals the time between two specific behaviours (number of replicates=6)

Behavioral events	Reproductive phases
First contact: male and female antennae are in contact for the first time.	Pre-contact (time between experiment start (i.e., female release) and first contact).
Female seizure: robustus male seizes the female between his pereopods in a “cage” state (sensu Correa et al. 2000).	Pre-seizure (time between first contact and female seizure).
Female spawning: female arches its abdomen inward and then moves a couple of steps backwards.	Pre-spawning (time between female seizure and female spawning).
Female liberation: robustus male releases the female from the cage.	Reproductive cage (time between female spawning and female liberation).
Spermatophore transfer (ST): robustus male transfers a spermatophore to the female’s ventral region of the abdomen.	Spermatophore transfer duration (time between the first and last spermatophore transfer).

A trial ended when the robustus male released the female from the reproductive cage. On some occasions, the robustus male interrupted the reproductive cage but then rapidly resumed this posture; these events were counted. A trial was discarded and repeated with new shrimps if a robustus did not cage the female within 60 min after the first contact or if a reproductive cage was interrupted before spermatophore transfer.

The behaviors of the five typus males in the tank were recorded and analyzed separately (multivariate analysis of variance (MANOVA): supplementary materials, Table S1) to confirm that they were independent of predation risk and robustus age and that any potential effects by typus males on the behavior of robustus males were similar among the treatments. The behavior of the typus males was, however, not the focus of our study and is therefore not further discussed.

Data analysis

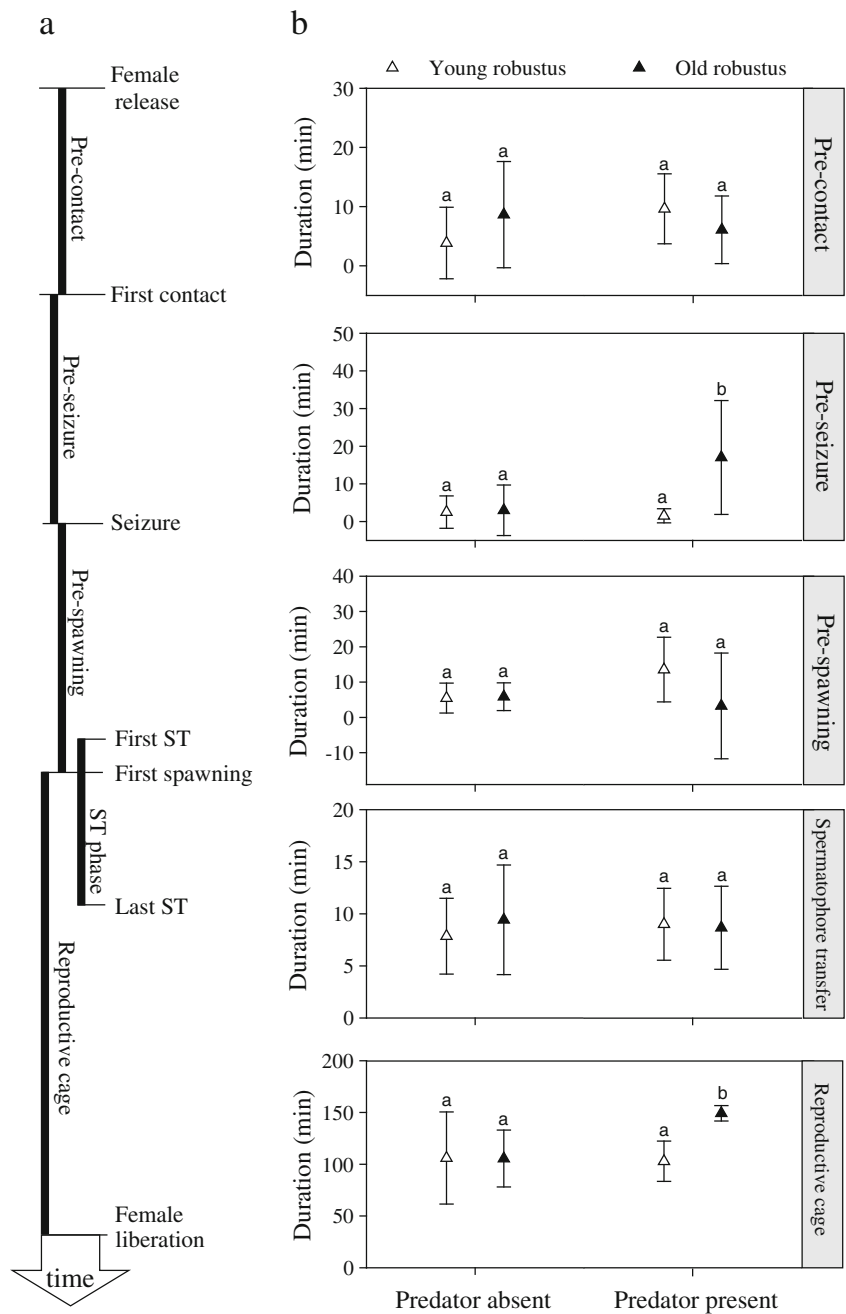
A MANOVA was run to test the null hypotheses that predation (predator absence vs. presence), age (young vs. old), and their interaction (independent variables) did not influence shrimp-mating behaviors (dependent variables, see Table 1). When necessary, data were Box-Cox-transformed to ensure homogeneity of variances (Sakia 1992). If the MANOVA was significant at the α -level error of 5 %, univariate ANOVAs were run independently to test the effects of the independent variables and their interactions on each variable. When an ANOVA was significant, pairwise comparisons of estimated marginal means were performed ($\alpha=5$ %) to test which treatment combinations differed significantly from each other using a sequential Bonferroni correction to account for multiple comparisons (Quinn 2002).

Differences in the number of robustus males that interrupted the reproductive cage in relation with robustus age and predation were not tested statistically because assumptions for contingency tables (>25 % of counts are <5 and none <1, Yates et al. 1999) were not met due to the small sample size for each treatment combination ($n=6$). All statistical analyses were performed using SPSS v. 18.

Results

In all but one trial (old robustus and predator present), at least one typus male made contact with the receptive female before robustus males. These first contacts by typus males occurred quickly, within 1.0 ± 0.7 min (mean ± 95 % confidence intervals, $n=23$) after a trial had begun. In most (83 %) of the trials, at least one typus male briefly maintained the female in the cage position and transferred one to three spermatophores. However, females never started to spawn when seized by typus males, which were dislodged readily by robustus males once these seized the female. In all treatments, robustus males

Fig. 1 **a** Ethogram showing the chronology (not to scale) of the different mating phases (variables) used in the analysis. **b** Mean ($\pm 95\%$ confidence interval) duration of pre-contact, pre-seizure, pre-spawning, spermatophore transfer (ST), and reproductive cage phases in relation to predation risk and the age of robustus males. Different letters above error bars indicate subset means that differ at the level of error 5 % (pairwise comparison of the estimated marginal means of the ANOVA model)



guarded the female, which always spawned after robustus started to transfer spermatophores.

The MANOVA revealed an overall effect of the interaction between predation risk and robustus age on all mating behaviors of robustus males and females together (Table 2). More specifically, time of first contact between robustus males and females ranged from 0.1 to 19.5 min (7.0 ± 2.6 min, $n=24$), and was affected neither by predation risk ($P=0.43$) nor by age of robustus ($P=0.90$; graph “Pre-contact” in Fig. 1b and Table 3).

The interaction between predation risk and robustus age influenced the duration of the pre-seizure phase ($P=0.02$;

Table 2 Results of the two-way MANOVA that tested the effects of predation risk, age of robustus males and their interaction on the duration of male and female mating behaviors

Factors	<i>F</i> (Pillai's trace exact test)	<i>df</i>	Error <i>df</i>	<i>P</i>
Predation	2.55	5	16	0.07
Age	1.54	5	16	0.23
Predation \times age	3.53	5	16	0.02

P values in bold are significant at the level of error $\alpha=5\%$

MANOVA multivariate analysis of variance

Table 3 Results of the two-way ANOVA ($n=6$) which tested the effects of predation risk and age of robustus males on each mating phase (variables)

Mating phases	Factors	df	MS	F	P
Pre-contact phase	Predation	1	15.68	0.36	0.55
	Age	1	2.41	0.06	0.82
	Predation×age	1	104.17	2.41	0.14
Pre-seizure phase (Box-Cox)	Predation	1	11.00	3.91	0.06
	Age	1	7.55	2.68	0.12
	Predation×age	1	19.61	6.97	0.02
Pre-spawning phase (Box-Cox)	Predation	1	45.38	0.54	0.47
	Age	1	146.03	1.73	0.20
	Predation×age	1	170.67	2.02	0.17
Spermatophore transfer phase	Predation	1	0.24	0.02	0.90
	Age	1	2.28	0.14	0.71
	Predation×age	1	5.42	0.33	0.57
Reproductive cage phase	Predation	1	2301.04	3.16	0.09
	Age	1	3151.04	4.33	0.05
	Predation×age	1	3290.04	4.52	0.04

Method used for data transformation is in parentheses. Values in bold are significant at the error level of 5 %

Table 3 and graph “Pre-seizure” in Fig. 1b): old robustus males seized the female later under predation risk (17.0 ± 15.9 min, $n=6$) than in the absence of a predator (3.0 ± 6.7 min, $n=6$, $P<0.01$; see Table S2) and after young robustus males, in which the timing was independent of predator presence (1.5 ± 2.0 min, $n=6$) or absence (2.5 ± 4.3 min, $n=6$; Fig. 1b).

Females initiated spawning 8.4 ± 2.0 min ($n=23$) after being seized by robustus males, except for one female which started to spawn 11.5 min after being seized by a typus male. After 19 min, that female disrupted the cage with the typus and was seized 5 min later by the robustus male and resumed spawning a few seconds after. The duration of the pre-spawning phase was neither affected by predation risk ($P=0.47$) nor by the age of robustus ($P=0.20$; Table 3 and graph “Pre-spawning” in Fig. 1b).

The spermatophore transfer phase lasted from 2.5 to 18.5 min (8.7 ± 1.6 min, $n=24$) and was affected neither by predation risk ($P=0.90$) nor by the age of robustus ($P=0.71$; Table 3 and graph “Spermatophore transfer” in Fig. 1b). The number of spermatophores transferred per robustus male ranged from three to 11 (6.5 ± 0.9 min, $n=24$).

Under predation risk, old robustus males never interrupted the cage state, whereas four of the six (67 %) young robustus interrupted the cage state, one to three times each, before the female spawning phase ended. Neither old nor young robustus interrupted female guarding when no predator was present. Old robustus males maintained the female in the reproductive cage for longer in the presence (148.5 ± 5.9 min, $n=6$) than in

the absence (105.5 ± 20.9 min, $n=6$, $P=0.01$; Table S2) of a predator and overall longer than young robustus (see graph “Reproductive cage” in Fig. 1b and Table 3).

Discussion

Our results were consistent with the prediction that, in the presence of a predator, old robustus *R. typus* males maintain females in the reproductive cage longer than younger counterparts do, suggesting that older males (with low RRV) accept greater risk during the mate-guarding phase. Young robustus males interrupted female guarding several times in the presence of a predator, indicating that males perceive and respond to predation risk during mate guarding. Older robustus males, on the other hand, never interrupted the reproductive cage before the female had finished spawning, which suggests that once they have initiated a mating, old males accept greater risk than younger males do during mate guarding. These results are consistent with the “terminal investment” hypothesis, which predicts that reproductive efforts increase with decreasing future mating opportunities (Williams 1966; Pianka and Parker 1975). Other studies on amphipods and water striders found, on the other hand, reduced mate-guarding duration under predation risk (Dunn et al. 2008; Sih et al. 1990), but did not take into account individual life history, which might have affected risk-taking decisions among mates with different RRV.

In mate-guarding species, mortality is generally greater in one or both members of a pair compared to unpaired individuals (e.g., Arnqvist 1989; Fairbairn 1993; Jivoff 1997; Jormalainen 1998; Rodríguez-Muñoz et al. 2011). Therefore, the frequency or duration of pair guarding is often reduced under greater predation risk (e.g., Sih et al. 1990; Travers and Sih 1991; Oku and Yano 2008). In *R. typus*, paired mates are less mobile and thus are probably less conspicuous to predators than during pre-mating phases when they move over comparatively large distances (Dennenmoser and Thiel 2007). However, the pair-guarding phase lasts substantially longer (about tenfold) than pre-copulatory phases, and most likely is not free of risk for the paired mates. In addition, in our experiments, robustus males seized females outside refuges. This is often observed in the field (Thiel and Correa 2004; NCO, personal observation and Fig. S1a, b, electronic supplements). This suggests that paired males are under greater predation risk than unpaired individuals are which usually aggregate in large groups inside holes and crevices (Ory et al. 2012 and Fig. S1b).

Lower mortality of paired females is often due to the assumption that males are more vigilant to detect predators (Artiss and Martin 1995) or are more exposed to predators (Gwynne 1989; Rodríguez-Muñoz et al. 2011). For example, Sivinski (1980) discussed that lower mortality of paired

female stick insects *Diaperomera veliei* (Heteronemiidae) was attributable to the exposed dorsal position of mating males, which are more likely to be captured by predators than are the females underneath. In *R. typus*, males are on top of the female that they cover almost entirely (see Fig. S1 and Fig. 3 in Correa et al. 2000). It is therefore possible that males are eaten first when the pair is attacked by a predator, which may explain, at least in part, why robustus males were found more often in fish stomachs than expected given their frequency in the foraging environment (Ory et al. 2012).

Prolonged pair guarding increases female (and its brood) survival but also allows the females to finish spawning, after which they are unreceptive and cannot be fertilized by other males (e.g., Jivoff 1997). The risk that males take when guarding females may thus enhance the success of that specific reproductive event. Rodríguez-Muñoz et al. (2011) found that wild cricket males that guard females are more vulnerable to predators than their mate but gain greater paternity than do non-guarding males because they are more attractive to females and ensure greater survival of their brood. In our experiment, old robustus males probably kept the female longer in cage to ensure successful fertilizations of all eggs as well as survival of the female. Greater predation risk incurred by older males during prolonged reproductive guarding may thus be balanced by greater reproductive success of what is likely to be one of their last reproductive events (Fig. 2).

Our experiment showed that the time of first contact between robustus males and females was independent of predation risk and robustus age and was similar to that found by other studies on *R. typus* (van Son and Thiel 2006; Dennenmoser and Thiel 2008). Those two studies also found that the time of first contact was not influenced by predation risk, robustus mating history, or intrasexual competition, which indicates that robustus males have stereotypic behaviors during the pre-contact phase. Males of decapod shrimps use their antennal flagella to recognize sex pheromones on the body surface of receptive females (e.g., Bauer 2011). First contact with females appears to be critical for males to determine whether the female is receptive, and evolutionary processes may have shaped, during this phase, stereotypic male behaviors that are not influenced by age or external (predation, competition) factors.

Once having become aware of the presence of a receptive female, the behaviors of old and young males were seen to diverge in the presence of a predator. The presence of a predator did not affect the time required by young robustus males to seize the female, whereas old robustus males delayed female seizure, possibly to carefully assess potential threats before engaging in long copulatory guarding, during which they are likely under high predation risk (see discussion above). This result suggests that risk assessment is a behavior that males acquire with age, probably from previous direct encounters with predators (Lönnstedt et al. 2012; Niemelä et al. 2012) or through social learning (Brown and Laland 2003; Frost et al.

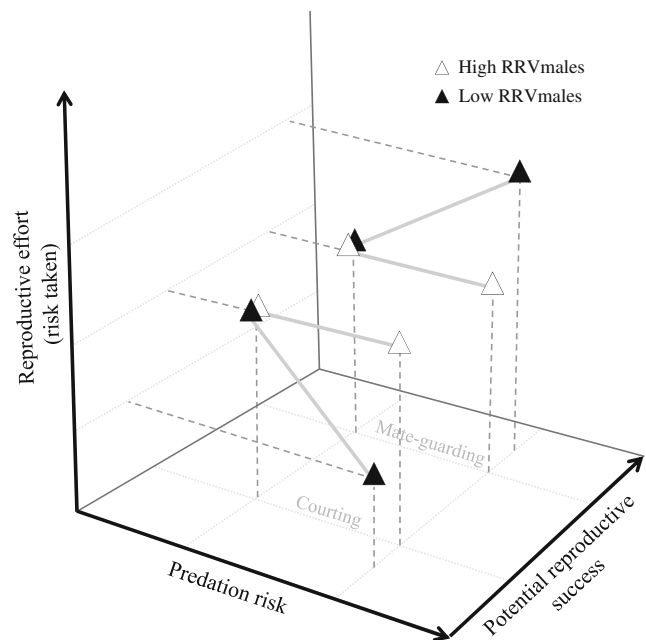


Fig. 2 Theoretical model predicting changes in reproductive effort (risk taken) of males with different RRV in function of increasing predation risk and the respective potential reproductive success associated with the display of a given mating behavior. The model is based on the results from our study which showed that males with low and high RRV exhibit similar reproductive effort in the absence of a predator. Under the threat of predation, males with low RRV take fewer risks when courting (potentially conceding fertilization to competitor males during this mating event) but more risk during mate guarding (increasing reproductive success for this reproductive bout). Males with low RRV may increase their reproductive effort (risk taken) according to the potential reproductive success associated with specific mating behaviors

2007; Lönnstedt et al. 2012). For example, fish individuals that had previous contact with predators experienced overall lower mortality than naïve individuals did (McCormick and Holmes 2006). The ability of individuals to adjust risky behaviors from past experience should thus be favored through selective processes (see Kemp 2002; Cameron et al. 2000).

Males that delay seizure take the risk that females are seized by another robustus male (Dennenmoser and Thiel 2007), thus potentially losing a reproductive opportunity. In our study, robustus males were only in competition with subordinate typus males which, although they can successfully transfer spermatophores and gain some fertilizations (Bailie et al. 2014), are always displaced by robustus males during direct conflicts (Correa et al. 2003). In addition, females actively remove parts of the spermatophores transferred by typus males (Thiel and Hinojosa 2003). The fitness costs for robustus males to lose some fertilizations to competing typus males may thus be low in comparison to the risk of being killed by a predator before having started copulation. Similarly, Artiss and Martin (1995) found that intrasexual competition had little effects on the breeding behaviors of male white-tailed ptarmigans compared to that of predation risk. In addition, Dennenmoser and Thiel (2008) found that

pre-seizure time did not vary in function of increasing competition (greater number of robustus present), which confirms that intrasexual competition does not have a strong influence on the timing of *R. typus* robustus males engaging in mate guarding.

Conclusions

This study highlights the importance of considering a life-history viewpoint in interpreting behavior, specifically in regard to the behavioral responses of prey to predation risk. The results of our experiment provide further support for the “terminal investment” hypothesis (Clutton-Brock 1984) because old dominant males with low RRV took more risk during mate guarding, probably to ensure fertilization and maximize their reproductive success. However, the older males hedged their bets: they did not display reckless risk-taking behaviors but rather cautiously assessed potential threats before engaging in possibly one of their last reproductive investments. Old individuals may have gained the experience to adjust their behaviors during one of their last investments more adequately than naïve counterparts would (“targeted reproductive effort hypothesis”; Cameron et al. 2000). More generally, our results suggest that individual reproductive efforts not only depend on intrinsic (age) and extrinsic (predation) factors, but are dynamic, reflecting specific trade-offs of particular mating behaviors (Fig. 2).

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Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Conflict of interest The authors declare that they have no competing interests.

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