

1 **Increased male mating success in the** 2 **presence of prey and rivals in a sexually** 3 **cannibalistic mantis**

4 5 **LAY SUMMARY**

6
7 Deciding when to approach a mate is critical for male mantises at risk of being cannibalised.
8 A male might do well to pounce when a female is distracted with prey, but what if a nearby
9 male has the same intention? In the Springbok mantis, we show that males mate faster and
10 with greater success when both prey and a rival are present, suggesting that mating decisions
11 depend on the dual threats of cannibalism and competition.
12

13 **ABSTRACT**

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15 Pre-copulatory sexual cannibalism—or cannibalism without mating—is expected to promote
16 the evolution of male strategies that enhance mating success and reduce the risk of
17 cannibalism, such as preferential mating with feeding females. However, sexual selection on
18 male competitiveness may alter male courtship decisions in the face of cannibalism risk. We
19 investigated the effect of prey availability and rival presence on male mating decisions in the
20 highly cannibalistic Springbok mantis, *Miomantis caffra*. We found that males approached
21 females more rapidly and mated more often in the presence of prey, suggesting that females
22 distracted with foraging may be less of a threat. The presence of a rival also hastened the
23 onset of copulation and led to higher mating success, with very large effects occurring in the
24 presence of both prey and rivals, indicating that intrasexual competition may intensify
25 attraction to foraging females. Taken together, our results suggest that pre-copulatory
26 cannibalism has selected for male preference for foraging females, and that males adjust their
27 mating strategy to both the risk of competition and the threat of cannibalism.
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29 Key words: sexual cannibalism, mantid, *Miomantis caffra*, mating tactics, sexual conflict,
30 prey availability, competition

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61 INTRODUCTION

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63 Understanding how animals maximise fitness while managing risk is a key focus of
64 behavioural ecology (Magnhagen 1991; Dall and Johnstone 2002; Dall 2010; Mathot et al.
65 2012). In sexually cannibalistic species—where females consume males prior to, during, or
66 immediately following copulation—males must balance the imperative to mate with the
67 danger of being eaten by females (Elgar 1992). This balancing act is particularly critical in
68 species where cannibalism occurs without mating (i.e., precopulatory cannibalism) because
69 males forfeit all current and future reproductive success if they are cannibalised (Elgar and
70 Schneider 2004).

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72 Males confronted with extreme costs of precopulatory cannibalism are expected to evolve
73 behavioural tactics to avert or avoid female aggression (Parker 1979; Elgar 1992; Schneider
74 2014). A common tactic emphasising distraction occurs when males preferentially approach
75 feeding females. Female feeding behaviour may be an important trigger for mating initiation
76 because females distracted by prey may be less likely to attack approaching males (Prenter et
77 al. 1994; Fromhage and Schneider 2005). In some orb-weaving spiders, males typically wait
78 for females to feed on prey before entering the web to attempt mating (Fromhage and
79 Schneider 2005). Similarly, some male mantids prefer feeding females (Scardamaglia et al.
80 2015) and mate with such females more readily (Gemeno and Claramunt 2006). This
81 suggests that females in prey-abundant environments may be less dangerous for males to
82 approach, and therefore the risks of cannibalism in such environments may be reduced.
83 However, the influence of prey abundance on male mating decisions with respect to
84 cannibalism risk is poorly understood.

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86 The presence of competitors could also influence how males interact with cannibalistic
87 females. Since most sexual cannibals are scramble competitors—where males compete to be
88 the first to find females and mate (Emlen and Oring 1977; Thornhill and Alcock 1983;
89 Herberstein et al. 2017)—the presence of male rivals is likely to feature prominently in a
90 male's calculus of risk (Prokop and Václav 2005). On the one hand, a male may use a
91 competitor as a decoy or 'sacrificial lamb', timing his approach to coincide with a female
92 stalking, attacking or eating the competitor. On the other hand, the presence of rivals may
93 intensify a male's motivation to mate, which may lead to faster mating approaches and

94 increased mating success, as occurs in non-cannibalistic taxa (Simmons 1986; Beani and
95 Turillazzi 1990; Price and Rodd 2006). Such a lack of caution may however lead to a higher
96 incidence of cannibalism due to hasty missteps (Stoltz et al. 2008). If males pay attention to
97 female foraging behaviour, the presence of prey could modulate competition among males in
98 non-additive ways. For example, if males approach feeding females faster than they approach
99 non-feeding females, the presence of a rival may intensify the speed of their approach,
100 resulting in either higher mating success or higher mating failure due to cannibalism. While
101 effects of female feeding behaviour and rival presence have been investigated in isolation,
102 how such factors interact to shape anti-cannibalism behaviours in males is currently unclear.
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104 The Springbok mantis, *Miomantis caffra*, is an excellent system for investigating effects of
105 prey and competitors on male mating decisions in response to the risk of cannibalism. As in
106 many other mantises, males are scramble competitors (Maxwell 1999). However, unlike most
107 cannibalistic species, pre-copulatory cannibalism occurs at an extremely high rate: more than
108 60% of inter-sexual encounters end in cannibalism without mating, one of the highest known
109 natural rates of cannibalism (Walker and Holwell 2016). Males have limited capacity to
110 assess the likelihood of being attacked since female aggression is not consistent within
111 individuals (Fisher et al. 2020), and is uninfluenced by female body size, condition, or
112 feeding regime (Walker and Holwell 2016). Females are also facultative parthenogens which
113 means they can produce viable offspring asexually without mating, via parthenogenesis
114 (Walker and Holwell 2016). This unique confluence of traits is expected to impose strong
115 selection on males to evolve tactics that, on the one hand, increase their competitive edge
116 against rivals, and, on the other, mitigate the risk of mating failure due to cannibalism.
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118 We conducted a laboratory experiment on *M. caffra* in which the presence of prey and the
119 presence of a rival were simultaneously manipulated. We hypothesised that males would pay
120 attention to female feeding behaviour by approaching females faster and mating more
121 frequently when prey were present. We also suspected that competition would increase the
122 motivation of males to mate, with the fastest onset of sexual contact occurring in the presence
123 of both prey and a rival. Due to the distracting nature of prey, we further predicted that
124 competition would enhance male mating success when prey were present, but would
125 exacerbate the incidence of cannibalism when prey were absent.

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128 **METHODS**

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130 To investigate the influence of rival and prey presence on mating and cannibalism, we
131 performed a fully factorial mating experiment consisting of two interacting treatments that
132 manipulated the presence of heterospecific prey and conspecific males. We placed individual
133 adult virgin females that had not yet oviposited ($n = 76$; 19 females per treatment
134 combination) into separate 30 x 30 x 30 cm mesh enclosures containing a bunch of artificial
135 plastic leaves and introduced either one or two adult males ('rival treatment'), and either 40
136 house flies or no flies ('prey treatment'). To prevent confounding due to differences in female
137 satiation levels between the prey treatment groups, females in the 'prey absent' group were
138 each housed with 40 flies for the 12 hours immediately prior to the experimental trial, while
139 females in the 'prey present' group were provided with 3 flies during this same period.
140 Observations of mating and/or cannibalism were made every hour for 8 hours. The
141 experiment was conducted in several blocks over multiple days due to space constraints. All
142 mantises were obtained as juveniles from numerous locations in Auckland, New Zealand.

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144 To analyse the likelihood of mating and cannibalism, we used generalised linear models
145 (GLMs) with binomial error structures and logit link functions. Mating outcome and
146 cannibalism outcome were treated as separate binary response variables, and rival treatment,
147 prey treatment and their interaction were included as fixed effects. A Cox proportional
148 hazards regression model was used to assess treatment differences in the onset of mating.
149 Latency to mate (measured in hours) was the response variable, with rival treatment, prey
150 treatment, and their interaction fitted as fixed effects. Individuals that did not mate were
151 treated as censored observations.

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153 We used likelihood ratio tests to assess the significance of fixed effects in all models. This
154 was done by removing each fixed effect from a reduced model that had nonsignificant
155 higher-level interactions removed. The significance of interactions was similarly assessed by
156 removing interaction effects from the full model. Trial date was initially included as a
157 categorical covariate but was later excluded from all analyses as no block effects were
158 detected ($-8.911 \leq \chi^2 \leq 7.656$, $0.780 \leq P \leq 0.865$). For effect sizes of mating success,
159 we report standardised mean differences (d) and 95% confidence intervals (CI) using the

160 probit transformation for binary response data (Glass et al. 1981). We report hazard ratios
161 (HR) and their 95% CIs for mating onset effect sizes.

162

163 RESULTS

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165 Males initiated mating nearly 4 times quicker when prey were present (Cox model: HR
166 = 3.799, CI = 1.588 to 9.088; analysis of deviance: $\chi^2 = 10.359$, $P = 0.001$; Figure 1),
167 and 3 times quicker when a rival male was present (Cox model: HR = 2.968, CI =
168 1.285 to 6.857; analysis of deviance: $\chi^2 = 7.123$, $P = 0.008$; Figure 1). Speed was
169 enhanced by the presence of both factors. When a rival was present, the addition of prey
170 increased the speed of approach by 4 times (HR = 4.034, CI = 1.446 to 11.260; Figure 1),
171 and when prey were present, the addition of a rival increased the speed of approach by nearly
172 6 times (HR = 5.587, CI = 1.825 to 17.100; Figure 1). By comparison, when only a rival
173 was present, mating onset was less than twice as fast as when no rival or prey were present
174 (HR = 1.770, CI = 0.423 to 7.410; Figure 1), and the presence of only prey had a near
175 equivalent effect on mating onset as the presence of no rival or prey (HR = 1.322, CI =
176 0.296 to 5.907; Figure 1). Despite the pattern of interaction suggested by these effect sizes
177 and CIs, there was no significant interaction effect between prey and rival presence in the
178 model (Cox model: HR = 3.068, CI = 0.500 to 18.821; analysis of deviance: $\chi^2 = 1.427$,
179 $P = 0.232$).

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181 The incidence of mating increased 171% in the presence of prey (mating incidence: prey
182 present: 19/38, prey absent: 7/38; $d = 0.899$, CI = 0.289 to 1.510 ; GLM coefficient =
183 1.639; analysis of deviance: $\chi^2 = -9.460$, $P = 0.002$; Figure 2), and 125% in the presence
184 of a male rival (mating incidence: rival present: 18/38, rival absent: 8/38; $d = 0.739$,
185 CI = 0.138 to 1.339; GLM coefficient = 1.391; analysis of deviance: $\chi^2 = 6.7585$,
186 $P = 0.009$; Figure 2). Prey and rival presence had large interactive effects. The addition of a
187 rival increased mating success by 180% when prey were present (mating incidence: rival with
188 prey: 14/19, no rival with prey: 5/19; $d = 1.267$, CI = 0.409 to 2.125; Figure 2), but only
189 33% when prey were absent (mating incidence: rival without prey: 4/19, no rival or prey:
190 3/19; $d = 0.199$, CI = -0.732 to 1.129; Figure 2). Similarly, the presence of prey
191 enhanced mating success by 250% when a rival was present ($d = 1.257$,

192 CI = 0.345 to 2.169; Figure 2), but only 67% when a rival was absent ($d = 0.370$, CI =
193 -0.542 to 1.281 ; Figure 2). Although the effect sizes and CIs of these pairwise comparisons
194 suggest that prey and rival presence enhanced mating success only when they occurred
195 together, there was no significant interaction effect according to the model
196 (GLM coefficient = 1.707 ; analysis of deviance: $\chi^2 = -2.295$, $P = 0.130$).

197 Cannibalism was observed in 2 out of 76 trials, and its occurrence was unaffected by any
198 treatment ($-17.676 \leq$ GLM coefficient ≤ 35.351 ; analysis of deviance: $-2.827 \leq \chi^2 \leq 0$,
199 $0.093 \leq P \leq 1$). We observed no incidences of females eating one male while
200 simultaneously copulating with the other.

201

202 **DISCUSSION**

203

204 Our results support the idea that sexually antagonistic selection favours the evolution of male
205 strategies that prevent sexual cannibalism and enhance mating success (Elgar 1992;
206 Schneider and Lubin 1998; Elgar and Schneider 2004). We found that matings were initiated
207 more often and more rapidly in the presence of prey, suggesting that males use female
208 foraging behaviour as a cue to determine the safest time to approach—a common male
209 strategy in sexually cannibalistic taxa (Prenter et al. 1994; Elgar and Fahey 1996; Fromhage
210 and Schneider 2005; Gemeno and Claramunt 2006). Although males were probably attracted
211 to foraging females because of the lower risk they posed, we found no difference in the
212 incidence of cannibalism among treatments. Indeed, rates of cannibalism were significantly
213 lower than those previously reported for this species—a finding likely to be driven by the
214 extremely high satiation levels experienced by females in our experimental design.

215 Nonetheless, as predicted under scramble competition, males responded to the presence of a
216 rival by approaching females faster and more frequently. This effect appeared to depend on
217 the presence of prey: males with both rivals and prey present initiated mating 4 times faster
218 and were 3.5 times more successful than those with only rivals. Taken together, our results
219 illustrate how the risk of mating failure due to precopulatory cannibalism can alter selection
220 on male mating decisions in context-dependent ways, and highlights the potential for sexual
221 selection to modulate antagonistic interactions in sexually cannibalistic taxa.

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223 Our results suggest that males pay attention to the feeding behaviour of females when
224 deciding when to initiate mating. Such a strategy has been suggested for other cannibalistic
225 taxa where males preferentially approach females that are actively handling or eating prey
226 (Prenter et al. 1994; Fromhage and Schneider 2005; Gemeno and Claramunt 2006). However,
227 it is known that males can discriminate between well-fed and hungry females (Barry et al.
228 2010; Brown et al. 2012). Thus, feeding females could be more attractive not because prey-
229 handling makes them less able to attack but because feeding provides a cue to males that
230 females are becoming satiated and therefore less dangerous (Avigliano et al. 2016). Our
231 experimental design accounted for this possibility by providing females with equivalent
232 access to large numbers of prey immediately before or during trials. This meant that any
233 difference in male approach in the presence versus absence of prey was unlikely to be due to
234 differences in female hunger. We found that matings were initiated more frequently and more
235 quickly when females were actively foraging (i.e., not satiated the previous day), suggesting
236 that, in this case, males assessed the risk of cannibalism using cues associated with female
237 foraging behaviour rather than perceived hunger levels. These results lend strong support to
238 the idea that distraction is an important signal for mating initiation in cannibalistic taxa
239 (Maxwell 1998; Bilde et al. 2006; Uhl et al. 2015; Toft and Albo 2016). However, it is likely
240 that males pay attention to the entire predation sequence when timing their approach, with
241 certain behavioural cues provoking greater response than others (Scardamaglia et al. 2015).
242 Finer-scale observations would be a valuable next step in assessing the relative importance of
243 specific behaviours, such as stalking, striking and feeding, in mating initiation.

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245 Our results are broadly consistent with the prediction that competition to fertilise eggs
246 hastens the onset of mating in protandrous mating systems (Darwin 1871; Thornhill and
247 Alcock 1983; Herberstein et al. 2017). Males in our experiment increased their mating effort
248 in the presence of a rival by initiating matings more rapidly and more frequently. However,
249 rival presence did not alter the incidence of cannibalism. Thus, our results provide no
250 evidence that enhanced motivation to mate under competition causes males to misjudge the
251 risk of cannibalism by approaching females too hastily. This is in contrast to the red back
252 spider in which the presence of a rival increases the incidence of precopulatory cannibalism
253 by causing males to spend less time in premating courtship than is necessary to convince
254 females to mate (Stoltz et al. 2008). However, the low rate of cannibalism in our study was
255 probably due to all females being well satiated rather than because of the presence or absence

256 of male rivals. How competition for females of differing hunger levels affects cannibalism
257 risk therefore remains an open question.

258

259 We predicted that the presence of prey could modulate male-male competition for mates if
260 mating tactics are influenced by female feeding behaviour. We found very large effects when
261 both a rival and prey were present, and small effects when only a rival or prey were present,
262 indicating that male mating success is enhanced by the concurrent presence of both cues. This
263 suggests that males may experience a higher risk of competition when females are distracted
264 with foraging, and so approach faster to avoid rivals reaching such females first, resulting in
265 higher mating success. These results highlight the general importance of considering a range
266 of realistic ecological contexts for male anti-cannibalism strategies. Staged experiments that
267 fail to account for important sources of ecological variation (such as the density of prey and
268 competitors) may over-estimate cannibalism rates and under-estimate the effectiveness of
269 male counter adaptations. Further exploration of the influence of prey abundance and quality
270 as well as male abundance in natural populations (e.g., Rabaneda-Bueno et al. 2008) will be
271 necessary for understanding the adaptive significance of sexual cannibalism and its role in
272 sexually antagonistic coevolution.

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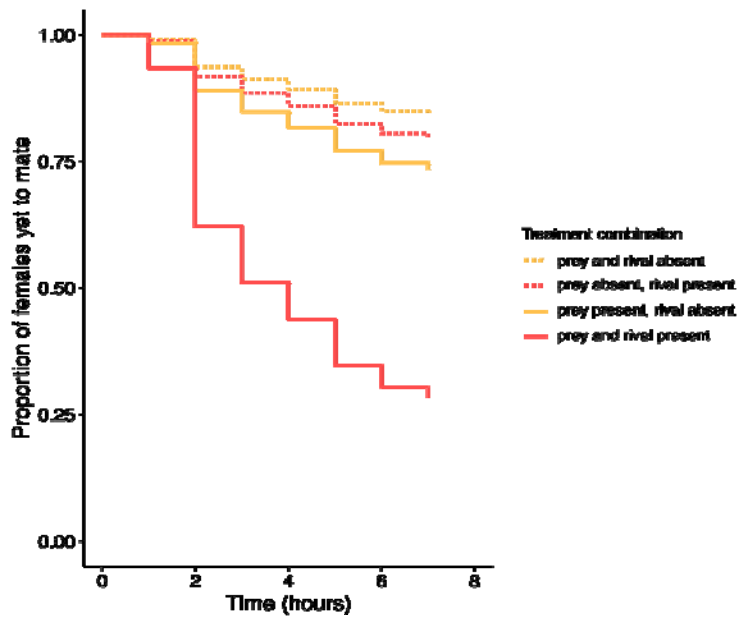
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381 **Figure 1.**

382 Survival curves showing the proportion of females remaining unmated over the duration of
383 mating trials. Censored observations are not depicted.

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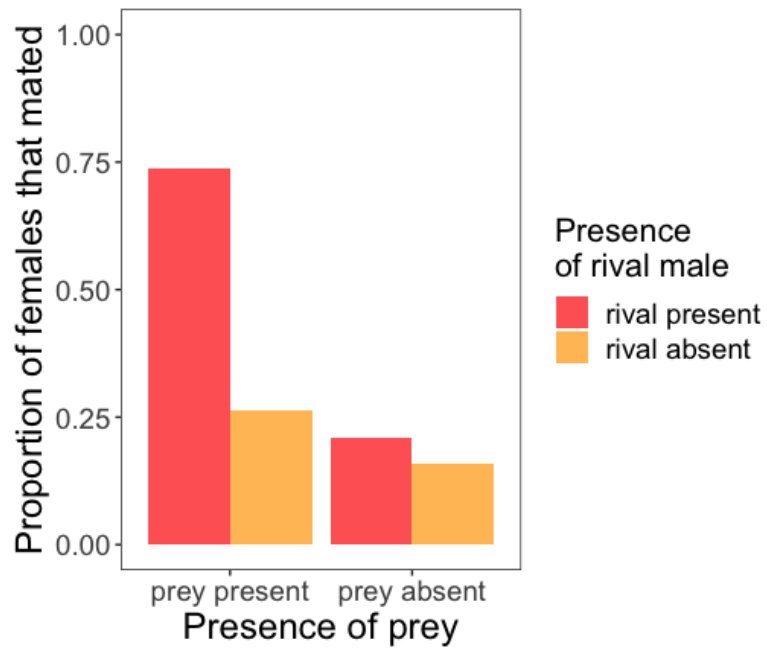
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402 **Figure 2.**

403 Bar graph showing the proportion of mating trials that ended in mating.



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