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Reproductive phenology and female mating frequency of the praying mantid *Tenodera angustipennis* in western Japan

Running title: Reproductive phenology of a praying mantid

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Abstract

1. The timing and frequency of female mating are important determinants of male reproductive success. Elucidating reproductive phenology is crucial to understand the evolution of mating behavior and mating systems.

2. Mate encounter rate is a key variable for understanding the evolutionary consequences of sexual cannibalism. However, we know remarkably little about female mating frequency in wild populations in mantids, charismatic insects that exhibit sexual cannibalism.

3. We examined the reproductive phenology of a wild population of the sexually cannibalistic praying mantid *Tenodera angustipennis*, and paid special attention to female mating frequency.

4. Field surveys throughout two reproductive seasons were combined with survival model analysis to estimate the phenology of eclosion, adult sex ratio, female first mating, and oviposition, allowing quantification of time windows for reproductive maturation and female mating.

5. Genetic paternity analysis using newly developed microsatellite markers revealed that females mated with two to six males on average before oviposition in the wild.

6. The results provide a comprehensive record of the reproductive phenology and female mating frequency in a wild mantid population, and insight into the evolution of male mating behavior under sperm competition and sexual cannibalism.

Keywords

microsatellite, polyandry, paternity, sexual cannibalism, sperm competition, survival analysis

Introduction

Sexual selection drives the evolution of male mating traits, and the timing and frequency of female mating are important determinants of male reproductive success (Andersson, 1994). In insects, the length of period between female reproductive maturation and oviposition may determine how many males can mate with a female (i.e., polyandry), and more polyandry can lead to more intensive post-copulatory competition among males, and stronger post-mating sexual selection on male mating traits (Simmons, 2001). Thus, elucidating the reproductive phenology (i.e., timing, duration and seasonality of reproductive events) of organisms is crucial to understand the evolution of mating behavior and mating systems (Shuster & Wade, 2003).

Sexual cannibalism is the predation of potential or actual mating partners in one sex (mostly male) by the other sex (female) during mating. As a result, females may gain nutritional benefit (Birkhead *et al*., 1988; Barry *et al*., 2008; Welke & Schneider, 2012; Brown & Barry, 2016; c.f. Maxwell, 2000), but males may suffer large fitness costs due to a loss of future mating opportunities. Thus, sexual cannibalism can be a strong agent of sexual conflict (Elgar 1992; Elgar & Schneider 2004; Schneider 2014). Theory predicts that mate encounter rate is a key variable for understanding the evolutionary consequences of sexual cannibalism (Buskirk *et al*., 1984; Barry & Kokko, 2010). Thus, determining the mate encounter rate may provide insight into the evolution of sexual cannibalism. Most males of the sexually cannibalistic red back spider can mate with only one female due to high male mortality when moving between sedentary females (Andrade, 1996). Given the opportunity of male's additional mating is limited, fitness loss in cannibalized males diminishes, resulting in the resolution of sexual conflict and the evolution of male suicidal behavior facilitating sexual cannibalism (Andrade, 1996). By contrast, large fitness costs to the male due to sexual cannibalism may lead to counter-adaptation in the male, in which selection favors male

67 mating traits avoiding cannibalism (Moya-Larano *et al*., 2004; Fromhage & Schneider, 2005;
68 Gemeno & Claramunt, 2006; Lelito & Brown, 2006; Barry *et al*., 2009; Scardamaglia *et al*.,
69 2015; Kadoi *et al*., 2017). Mantid males are known to encounter multiple females in
70 experimental (Inoue & Matsura, 1983) and wild (Maxwell, 1998; Christensen & Brown,
71 2018) populations. Fitness gain by cannibalized males through increased offspring by
72 nutritional contribution is smaller than fitness loss by losing future mating (Brown & Barry,
73 2016). These results suggest that sexual cannibalism in mantids is not an adaptive suicidal
74 behavior but a result of sexual conflict.
75 Unlike male mate encounter rate, less is known about female mate encounter rate or
76 female mating frequency in sexually cannibalistic species, especially mantids. Because
77 females of *Pseudomantis albofimbriata* stop emitting pheromones attracting males after the
78 first mating, females are believed to be monogamous or engaging in very low levels of
79 polyandry in the wild (Barry *et al*., 2011). However, in a laboratory setting where males can
80 locate females visually, females can mate with multiple males (Barry *et al*., 2011). In a semi-
81 natural setting, females of the praying mantid *Tenodera angustipennis* mated with an average
82 of 1.8 (up to 4) males (Inoue & Matsura, 1983). Genetic analysis of paternity in a clutch
83 indicated that *Ciulfina klassi* females mated with one to four males in the wild, while
84 congeneric *C. rentzi* females were monogamous (Umbers *et al*., 2011). Similarly, 2 of 18
85 *Tenodera aridifolia* females were estimated to mate with two males (Watanabe *et al*., 2011).
86 Although these studies suggest that female multiple mating is possible, we still know
87 remarkably little about female mating frequency in wild mantid populations.
88 Herein, we investigated the reproductive phenology of a wild population of the
89 sexually cannibalistic *T. angustipennis*, paying special attention to female mating frequency.
90 Based on the previous record of encounter rate between the male and female (Inoue &
91 Matsura, 1983), we hypothesized that this species has a polyandrous mating system. Field

surveys were conducted throughout two reproductive seasons to characterize the phenology of eclosion, adult sex ratio, female first mating, and oviposition. Survival model analysis was performed to estimate the median times of reproductive events, from which we estimated time windows available for female reproductive maturation and multiple mating. Additionally, we constructed novel microsatellite markers for this species, and estimated female mating frequency based on wild-caught females and wild-collected oothecae. We discuss the mode of female multiple mating in the wild, the possibility of sperm competition, and implication to the evolution of sexual cannibalism.

Materials and methods

Field surveys

Tenodera angustipennis is widely distributed throughout south and east Asia, including the Japanese Archipelago. This species is univoltine, and common and inhabits open environments, such as grassland, cultivated fields, and riverbeds. Our research area was rice fields and surrounding grasslands in Kobe, Japan (34°49'38.0"N, 135°09'23.9"E, about 1500 m^2), where Canadian goldenrod *Solidago canadensis* and Japanese pampas grass *Miscanthus sinensis* are the dominant vegetation, in addition to cultivated rice *Oryza sativa*.

Field surveys were conducted for 2 or 3 h in the morning (8:30 to 10:30 or 11:30) from mid-August to the end of October over 2 years (2017, Aug. 17–Oct. 18; 2018, Aug. 18–Oct. 24) at approximately 2 week intervals. These periods encompassed the onset of adult emergence to the end of reproduction. In every survey, two to five collectors searched around the area for 2 to 3 h and collected nymphs, adults, and oothecae. The number of collected nymphs, male adults, female adults, and oothecae was recorded. We also recorded the number of mating pairs with or without sexual cannibalism. These surveys were performed along predetermined routes, but the discovery rate of mantids and oothecae seemed to depend on

117 collecting effort (i.e., the number and composition of collectors and survey time) because they
118 are cryptic (Fig. 1). This effect was corrected in the analysis (see below). Collected mantises
119 were transferred to the laboratory for analysis of mating status (see below) and other
120 behavioral studies (to be reported elsewhere). Thus, we removed collected individuals from
121 the wild population. This effect was assumed to be negligible because the study population
122 seems to be sufficiently large relative to our sample sizes.
123
124 *Female mating status*
125 Field-collected adult females ($N = 32$ in 2017 and $N = 61$ in 2018) were allowed to
126 oviposit in the laboratory to collect oothecae, which were used for genetic analysis of
127 paternity. Females were housed individually in a plastic jar (13 cm diameter × 10 cm high)
128 topped with cotton mesh, and fed two crickets (*Acheta domesticus*, 0.262 ± 0.0562 g, $N = 52$)
129 and sprayed with water three times per week. These were placed in incubators maintained at
130 25 °C with a 16 h light:8 h dark photoperiod. After oviposition, females were frozen at -
131 20 °C. Oothecae were individually stored in a small plastic cup (7 cm diameter × 3.5 cm
132 high), kept under the same conditions as adults, and then moved to 5 °C from November to
133 the following March. From the start of April, oothecae were kept at room temperature, and
134 hatched nymphs were collected and stored in 99% ethanol. Field-collected oothecae were
135 treated in the same manner.
136 To investigate female mating status, spermatheca of field-caught females were
137 dissected after oviposition. Spermatheca were removed from the female abdomen under a
138 stereo microscope (Leica EZ4HD) using fine forceps. Spermatheca were placed in a 1.5 mL
139 experimental tube with 200 μL particle-free water, incised by fine forceps, and vortexed.
140 After adding 800 μL of water and gently mixing, individual ejaculates stored in the

141 spermatheca were finally suspended in 1000 μL water. Ten 1 μL aliquots were placed on a
142 glass slide, dried, and examined for the presence of sperm using a stereo microscope.
143
144 *Genetic analysis of female mating frequency*
145 Eight polymorphic microsatellite markers were newly developed for *T. angustipennis*
146 (Table S1). Prior to this, we tested primers developed for other species, but one locus for the
147 congeneric *T. aridifolia* (Watanabe *et al*., 2011) was monomorphic, and none of the nine loci
148 for *Ciulfina rentzi* (Attard *et al*., 2009) were amplified in *T. angustipennis*. Since
149 polyneopteran insects including mantids are notorious for their large genomes (Koshikawa *et*
150 *al*., 2008), we focused on RNA sequences as a target for microsatellite identification (e.g., Du
151 *et al*., 2015; Wang *et al*., 2012; Zhang *et al*., 2012; Wang *et al*., 2015). Total RNA was
152 extracted from the head of an adult female using an RNeasy Mini Kit (Qiagen), and processed
153 using a TruSeq Stranded mRNA LT Sample Prep Kit (Illumina) for library construction.
154 Paired-end sequencing (2 × 101 bases) was performed using NovaSeq 6000 (Illumina),
155 resulting in 74,045 contigs (average 702.47 bases, total 52,014,029 bases) after *de novo*
156 assembly by Trinity (Grabherr *et al*., 2011). Microsatellites with dinucleotide to
157 hexanucleotide repeats were searched and PCR primer sequences were determined using
158 Msatcommander (Faircloth, 2018). As a result, 69 primer pairs were identified, and primers
159 were synthesized for 52 randomly selected loci and checked for amplification and
160 polymorphism based on 36 *T. angustipennis* individuals. Finally, eight loci were chosen with
161 respect to polymorphism and amplified length. Observed and expected heterozygosity were
162 computed, and Hardy-Weinberg equilibrium was tested based on 999 random
163 pseudoreplicates using GenAlEx 6.5 (Peakall & Smouse, 2012) (Table S1). Cross-species
164 amplification was also checked for *T. aridifolia* ($N = 17$), revealing that three of eight loci

(Tang25872, Tang26190 and Tang30982) were amplified and polymorphic. No loci were amplified for *Hierodula patellifera* ($N = 4$) or *Statilia maculata* ($N = 6$).

A total of 29 oothecae (7 from 27 oviposited by field-caught females in 2017, 3 of 12 field-collected oothecae in 2017, 19 from 59 oviposited by field-caught females in 2018, and 0 of 11 field-collected oothecae in 2018) hatched successfully and were subjected to genetic analysis of paternity based on eight microsatellite loci. We observed relatively low hatching rates, possibly due to the harsh overwintering conditions. Note that unmated females of *T. angustipennis* oviposit unfertilized eggs. Total DNA was extracted from ovipositing females and offspring hatched from oothecae ($N = 5$ to 31, mean ± s.d. = 22.9 ± 8.8) using a Wizard Genomic DNA Purification Kit (Promega). Multiplex PCR amplification of the eight loci was performed using fluorescently-labeled primers and a Multiplex PCR Assay Kit (Takara) with the annealing temperature of 60 °C. Amplified products were analyzed using an ABI3130xl genetic analyzer and GeneMapper software (Thermo Fisher Scientific).

The hypothesis that *T. angustipennis* has a polyandrous mating system predicts multiple paternity in a clutch. To examine this prediction, the paternity of offspring was estimated based on microsatellite genotypes of the mother and her offspring (for field-caught females) and those of offspring only (for field-collected oothecae). First, we calculated the number of fathers based on allele count; the maximum number of alleles among the eight loci in a clutch was divided by 2 (for diploid), 1 was subtracted (for the mother), and the number was rounded up to an integer. This approach is simple but it underestimates when the number of loci is small and allelic diversity is low. In addition, we also estimated the paternity of offspring using a likelihood method with COLONY ver. 2 (Jones & Wang, 2010). The rates of allelic dropout and other genotyping errors were both set to 0.01. Females and males were presumed polygamous and monogamous, respectively. Full-likelihood analyses were

189 performed with a ‘long’ run and allele frequency updating deactivated. The estimated number
190 of fathers for each clutch was recorded as the number of males mated with the female.
191
192 *Statistical analysis*
193 Since both the collecting effort per day (collection time and the number of collectors)
194 and the collecting ability of individual collectors varied, we attempted to correct these factors
195 to obtain the relative number of collected mantises per unit collecting effort. For the 2017
196 data, we simply corrected the number of mantises collected per day by dividing by collection
197 time and the number of collectors.
198 Variation in collecting ability among collectors could not be corrected because we did not
199 record the number of collected mantises for each collector in 2017. However, in 2018, we
200 recorded the number of mantises collected by each collector, from which we estimated the
201 variation in collecting ability among collectors. We constructed a generalized linear model
202 (GLM, log link and Poisson distribution) with the number of collected mantises per collector
203 per day as the objective variable, and the ID of collectors, the total number of collectors, and
204 the collection time each day as the explanatory variables. The log-transformed total number of
205 collected mantises per day was also included as an offset term. As a result, significant
206 variation in collecting ability was detected (Table S2). The coefficients estimated for
207 individual collectors provided a measure of collecting ability on a log-transformed scale (i.e.,
208 GLM with log link). Thus, we estimated the collecting effort per day as the sum of
209 antilogarithms of coefficients of individual collectors participating, and multiplied by the
210 collection time. Next, the number of mantises per day was divided by the collecting effort.
211 Since these estimates provide the relative number of collected mantises per unit collecting
212 effort, we can compare these among days in 2018.

We asked how long period is available for female multiple mating. In addition, we assessed how long period is required for female reproductive maturation, which is relevant to female nutritional requirement and tendency of practicing sexual cannibalism. To estimate the lengths of these periods, we estimated the phenology of eclosion, female first mating, and oviposition in the wild, by constructing parametric survival models. In the model of eclosion, captures of a nymph provided right censored data for the timing of eclosion, while those of an adult provided left censored data. Similarly, in the model of female first mating, captures of an unmated female provided right censored data for the timing of female first mating, while those of a mated female provided left censored data. In the model of oviposition, collection of oothecae provided interval data spanning from the day of the previous survey to the day of collection, during which oothecae were assumed to be oviposited. We included the year as an explanatory variable to examine variation among years. We also included sex as an explanatory variable in the model of eclosion to examine sex difference (i.e., the possibility of protandry). We compared assumptions of Weibull, exponential, Gaussian, logistic, log-normal, and log-logistic distributions, and the optimal distribution was selected by consulting the Akaike information criterion (AIC). Based on these models, we estimated the 2.5%, 25%, 50%, 75%, and 97.5% quantiles (i.e., days) of the events occurring. These analyses were performed by the *survival* function in R 4.1.1 (R Development Core Team, 2021). Additionally, to examine whether sex ratio deviated from 0.5, we performed binomial tests for each collection day.

If *T. angustipennis* has a polyandrous mating system, it is expected that female mating frequency increases with increasing time throughout the reproductive season. To examine this, we constructed a GLM (log link and Poisson distribution) with the estimated number of fathers as the objective variable and collection day, sample type (females in 2017, oothecae in 2017, or females in 2018), and the number of analyzed offspring as explanatory

variables. Field-collected oothecae in 2018 did not hatch (see above). All GLM analyses were performed using JMP ver. 14 (SAS Institute, 2018), in which overdispersion was corrected by the function implemented in the software.

Results

Reproductive phenology

We collected 498 individuals over the 2 years (2017 = 47 males, 32 females, 118 nymphs; 2018 = 108 males, 61 females, 132 nymphs). In both years, numerous individuals were collected from late August to mid-September, and then the number decreased (Fig. 2a, b). Very few individuals were recorded in August 24, 2017, probably due to low abilities of the collectors on this day. This motivated us to correct variation in collecting ability in 2018. We found a female with a spermatophore attached to the abdominal terminalia (i.e., just after mating), a female mounted by two males (Fig. 1), and a pair engaged in cannibalistic mating on September 27, 2017. We also found a pair engaged in cannibalistic mating on September 26, 2018.

Almost all individuals were still nymphs in mid-August. Eclosion started from late August, and almost all individuals had become adults by mid-September (Fig. 2c, d). The estimated median dates of eclosion were August 28.4 (± 2.03 s.e.) and 30.7 (± 2.01) for males and females in 2017, and August 29.1 (± 2.01) and 31.4 (± 1.20) for males and females in 2018 (Fig. 3). Although males tended to eclose earlier, there were no significant differences in the timing of eclosion between sexes and between years (Table 1).

The adult sex ratio tended to be biased to males during September, which differed significantly from the null hypothesis (i.e., 0.5) at the end of the month (Fig. 2e, f). The adult sex ratio (i.e., the frequency of males) then decreased in October, but there was no significant

departure from the null hypothesis. Fluctuations in sex ratio in early seasons were due to the small number of adults in the sample.

Mating status was examined in 82 (N = 26 in 2017; N = 56 in 2018) out of 93 (N = 32 in 2017; N = 61 in 2018) females. The remaining 11 females were failed at detecting the spermatheca due to technical problems. One female in 2018 with no observable sperm oviposited fertile eggs, and two females in 2018 were failed at examination but oviposited fertile eggs. These three females were recorded as mated. As a result, 46% (12 of 26) and 29% (16 of 56) of females were considered mated in 2017 and 2018, respectively. This result revealed that mated females were rare until mid-September, and the frequency started to increase thereafter (Fig. 2g, h). The estimated median dates of female first mating were September 25.6 (± 4.18) and 25.0 (±3.02) in 2017 and 2018, respectively. There was no significant difference in the timing of female first mating between years (Table 1).

Oothecae were first found from the end of September, and increased in October (Fig. 2i, j). The estimated median dates of oviposition were October 8.4 (± 3.21) and 8.1 (± 1.81) in 2017 and 2018, respectively. There was no significant difference in the timing of oviposition between years (Table 1).

Female mating frequency

As expected, *T. angustipennis* had a polyandrous mating system. Based on the simple allele count estimates, 62.1% (18/29) of analyzed clutches included multiple paternity, with 1.93 ± 0.88 fathers (mean ± s.d.). Based on maximum likelihood (ML) estimates, 96.6% (28/29) of analyzed clutches included multiple paternity, with 6.34 ± 3.29 fathers (Fig. 4). Thus, as expected, this simple method based on allele count may underestimate, but the results strongly indicate that females of this species frequently mate with multiple males.

286 Unexpectedly, the female mating frequency did not increase with increasing time
287 throughout the reproductive season, but included cases of high mating frequencies just after
288 the emergence of mated females (Fig. 4). The GLM explaining the ML estimates for the
289 number of fathers was marginally non-significant ($\chi^2_4 = 8.94$, $p = 0.063$). The effects of
290 collection day and sample type were not significant (collection day, $\beta = 0.008 \pm 0.007$, $\chi^2_1 =$
291 1.18, $p = 0.28$; sample type, $\chi^2_2 = 0.67$, $p = 0.72$). The effect of the number of analyzed
292 offspring tended to be positive ($\beta = 0.023 \pm 0.013$, $\chi^2_1 = 3.31$, $p = 0.069$), suggesting the
293 dependency of estimates on sample size. The GLM explaining allele count estimates of the
294 number of fathers was not significant ($\chi^2_4 = 1.65$, $p = 0.80$).
295
296 **Discussion**
297 We determined the reproductive schedule in a wild population of the praying mantid
298 *T. angustipennis* in western Japan. As expected from the hypothesis that this species has a
299 polyandrous mating system, we provided genetic evidence for female multiple mating with
300 estimates of female mating frequency in the wild. Our ML estimates of female mating
301 frequency were high relative to a previous study on this species (Inoue & Matsura, 1983) and
302 to a congeneric species (Watanabe *et al*., 2011). Mutations and genotyping errors could bias
303 estimation of parental assignment, but our estimation using Colony took these effects into
304 account (Wang, 2004; Wang & Santure, 2009). To our knowledge, this is the first
305 comprehensive record of female reproductive phenology and multiple mating in wild mantid
306 populations.
307 The estimated median times of eclosion and first date of female mating indicate that
308 adult females reach reproductive maturation at ~26 days after adult moult (Fig. 3). We know
309 from previous studies on mating behavior that new adults of this species take about a month
310 to mate (e.g., Kadoi *et al*., 2017), and our current results demonstrate that this is also the case

311 in the wild. A relatively long period to sexual maturation suggests that adult females require a
312 large amount of nutrients for their reproduction. Since variation in prey nutrients largely
313 influence female reproductive output (Matura & Morooka, 1983; Maxwell *et al*., 2010; Barry
314 & Wilder, 2013), foraging success in this period may be an important factor for female
315 reproductive fitness in this predatory insect. The requirement of a plentiful supply of nutrients
316 in this period may also be relevant to the evolution of sexual cannibalism because female
317 nutritional condition may influence the propensity of mate attraction (Lelito & Brown, 2008;
318 Barry, 2010) and subsequent occurrence of sexual cannibalism (Maxwell, 2000; Maxwell *et*
319 *al*., 2010; Barry, 2015). Since cannibalized males can constitute a significant amount of
320 female nutritional intake in the congeneric species *T. aridifolia* (Hurd *et al*., 1994; Brown &
321 Barry, 2016), it is warranted to investigate how sexual cannibalism contribute to the
322 nutritional intake and reproductive output of *T. angustipennis* females that require long time
323 for reproductive maturation.
324 The estimated median times for female first mating and oviposition indicate that
325 females require ~13 days from the first mating to oviposition (Fig. 3), suggesting that a 2
326 week window allows for females to mate with other males. We observed a possible case of
327 female multiple mating (Fig. 1), and our genetic analysis of paternity revealed that females
328 mated with multiple males in the field. Female mating frequency did not increase constantly
329 through reproductive seasons, as indicated by the non-significant effect of collection day in
330 the GLM explaining the number of fathers in a clutch (Fig. 4). This suggests that female
331 multiple mating occurs shortly after reproductive maturation, and then females may mate
332 infrequently. This is congruent with the fact that mated female mantids cease to emit
333 pheromones to attract males (Lelito & Brown, 2008; Barry *et al*., 2011). Thus, the time
334 window for female remating may be shorter than the above estimate. If this is the case, female
335 mating frequency likely depends on the local density of males that can reach the female

within this short time window. The large variation in female mating frequency (Fig. 4) might be explained by the possible variation in local male density. From the standpoint of the male, the opportunity to mate with a female may be restricted to a short time period after female maturation. The weak tendency of protandry (Figs. 2, 3), although non-significant in the survival model analysis (Table 1), suggest that males attain mating success by early eclosion, but the benefit is minimal due to large variation in the timing of female eclosion (Fig. 3).

When females mate with multiple males, sperm from different males compete for fertilization of the limited number of eggs through sperm competition (Simmons, 2001). The observed high rate of clutches including multiple paternity (62.1–96.6%) and the high frequency of female remating (1.93–6.34 males per clutch) indicate that males of *T. angustipennis* engage in moderate to strong sperm competition. Sexual selection via sperm competition is expected to favor offensive and defensive male traits that increase fertilization success (Simmons, 2001). In *Ciulfina klassi*, sexual selection operates on male genital morphology, which enables rapid sperm transfer to the female (Holwell *et al*., 2010). Specific male genital morphology may be beneficial for flushing out rival sperm from within the spermatheca, as an offensive adaptation to sperm competition. Sperm competition also provides insight into male adaptation to sexual cannibalism because a cannibalized male could increase his fitness in the context of competitive fertilization by expending more effort in his final mating (i.e., terminal investment) (Clutton-Brock, 1984; Andrade & Kasumovic, 2005). Sexually cannibalized males of *Pseudomantis albofimbriata* extend the duration of copulation, although this did not increase fertilization success in sperm competition in the double mating experiment (Barry *et al*., 2011). These males might expend more effort on mate guarding as a defensive adaptation to sperm competition. Nevertheless, little is known about sperm competition in mantids, including *T. angustipennis*, warranting further study.

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493

494 Figure legends

495

496 Fig. 1. A *Tenodera angustipennis* female mounted by two males in the rice field. Observed on
497 September 27, 2017.

498

499 Fig. 2. Phenology of the number of individuals collected (a, b), eclosion (c, d), sex ratio (e, f),
500 female mating status (g, h), and the number of oothecae collected (i, j). *p <0.05, **p <0.01
501 from binomial tests of sex ratio ($H_0 = 0.5$).

502

503 Fig. 3. Timing of eclosion, female first mating, and oviposition estimated by parametric survival
504 models. Median and 2.5%, 25%, 75%, and 97.5% quantiles are shown.

505

506 Fig. 4. Phenology of female mating frequency. Filled diamonds and circles refer to field-caught
507 females and field-collected oothecae in 2017, respectively. Open diamonds refer to field-
508 caught females in 2018.

509

510

511 **Table 1. Parametric survival models for estimating the phenology of eclosion, female first**

512 **mating, and oviposition in *Tenodera angustipennis***

513

	β	s.e.	z	p
Eclosion (distribution = logistic)				
Intercept	13.699	2.007	6.83	<0.0001
Sex (male/female)	-2.311	1.510	-1.53	0.13
Year (2018/2017)	0.666	2.029	0.33	0.74
Female first mating (distribution = log-logistic)				
Intercept	3.680	0.102	36.14	<0.0001
Year (2018/2017)	-0.016	0.127	-0.13	0.9
Oviposition (distribution = Weibull)				
Intercept	3.991	0.059	68.22	<0.0001
Year (2018/2017)	-0.007	0.068	-0.10	0.92

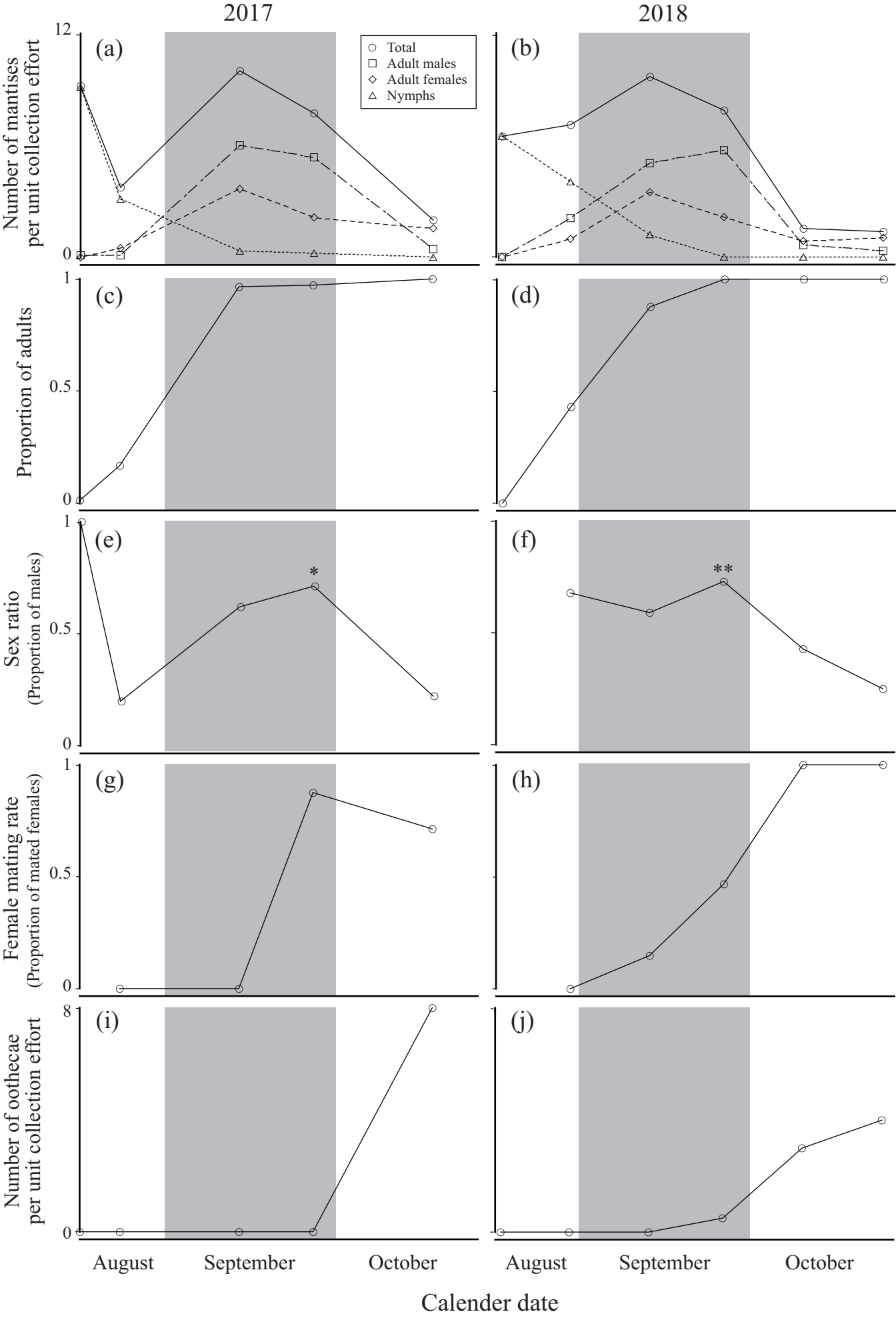
514

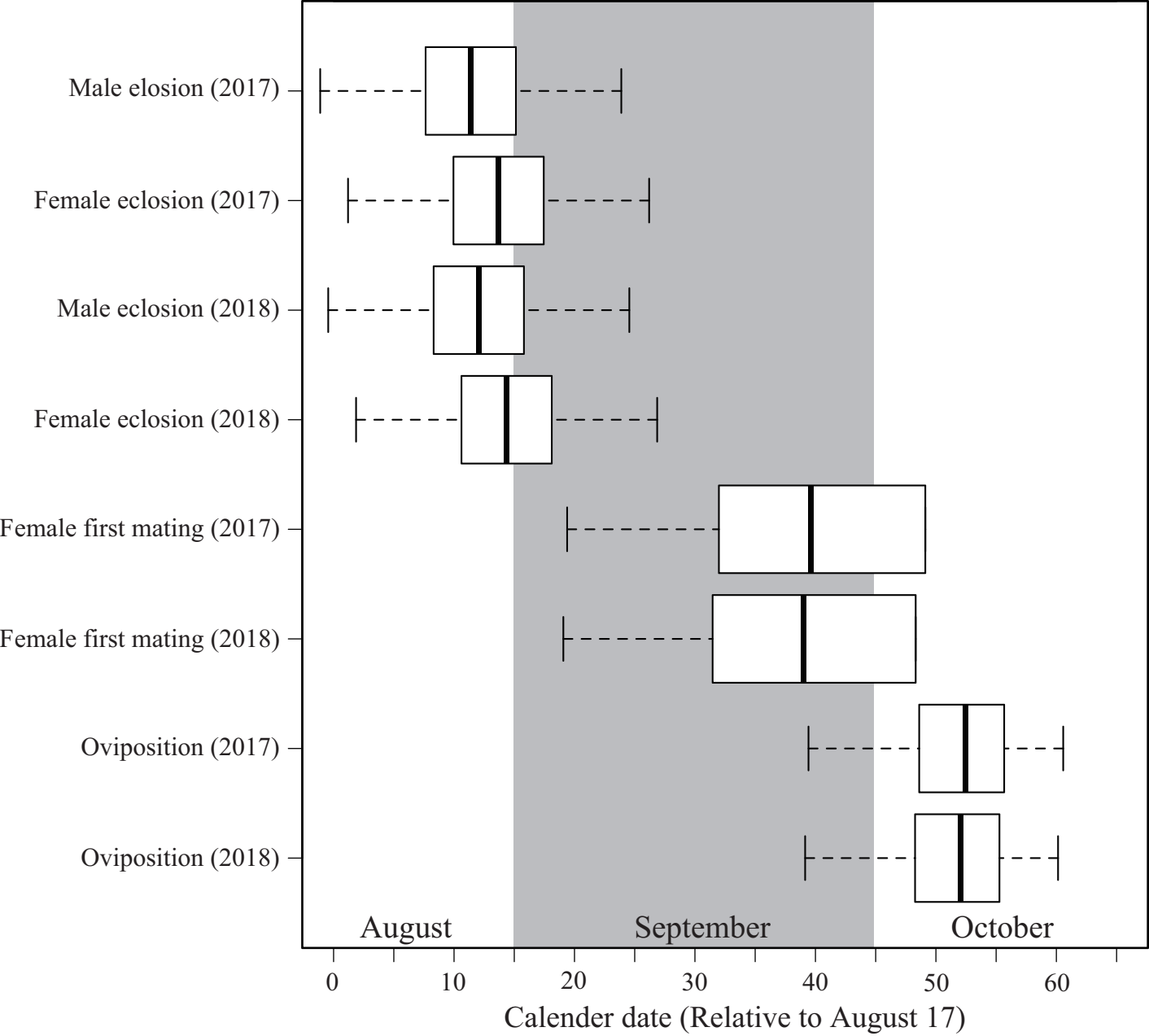
515

Legends of supplemental tables

Table S1. Characteristics of eight newly developed microsatellite markers in *Tenodera angustipennis*

Table S2. Generalized linear models explaining variation in collector ability


2017
2018
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
Total
Adult males
Adult females
Nymphs
Number of mantises per unit collection effort
Proportion of adults
Sex ratio (Proportion of males)
Female mating rate (Proportion of mated females)
Number of oothecae per unit collection effort
12
0
1
0.5
0
8
*
**
August
September
October
Calender date


Male elosion (2017)
Female eclosion (2017)
Male eclosion (2018)
Female eclosion (2018)
Female first mating (2017)
Female first mating (2018)
Oviposition (2017)
Oviposition (2018)
August
September
October
0
10
20
30
40
50
60
Calender date (Relative to August 17)

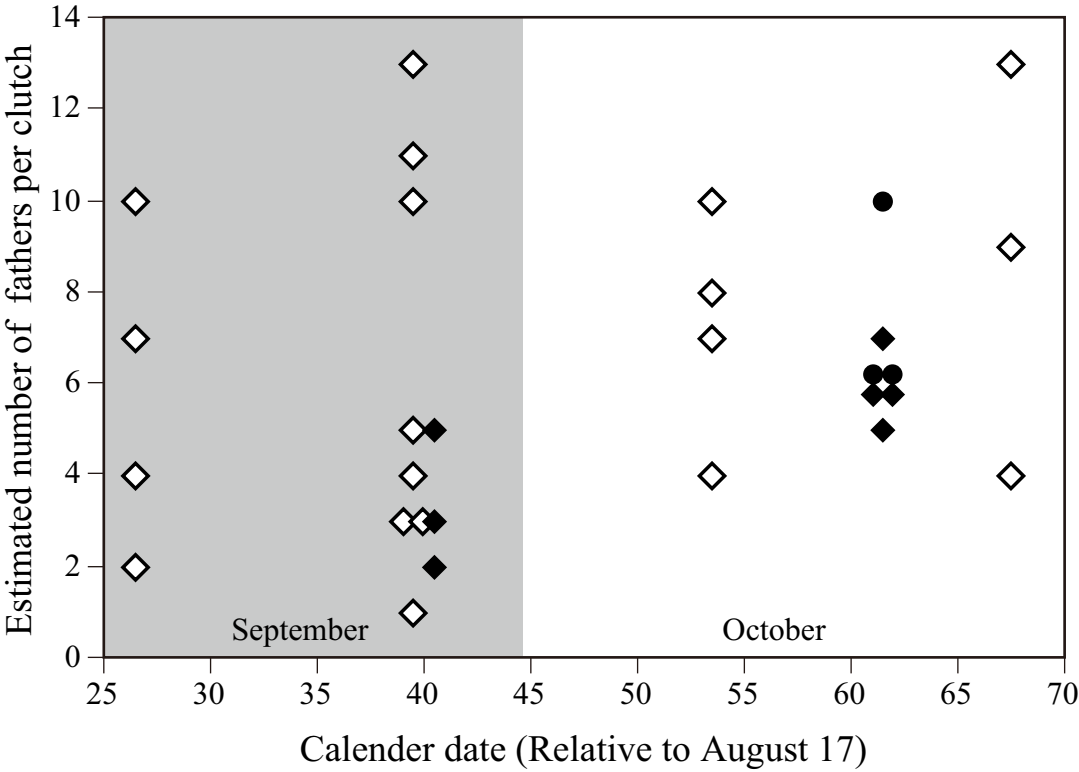

Estimated number of fathers per clutch
0
2
4
6
8
10
12
14
September
October
25
30
35
40
45
50
55
60
65
70
Calender date (Relative to August 17)

Table S1. Characteristics of eight newly developed microsatellite markers in *Tenodera angustipennis*

Locus	Forward primer	Reverse primer	Size range (bp)	N_a	H_o	H_e	*P* of HWE	Accession No.
Tang25872	CCGGCAAAGAGAAGTCGTTC	TCAATGCGCAGATCATCGC	138-168	9	0.528	0.767	< 0.001	LC655310
Tang26190	CACAGCTGACACAATGTTGC	ACAGCTCTACTCTCATGCTCC	373-410	4	0.629	0.511	< 0.001	LC655311
Tang26442	AGGGCGATCTTGACAAACAC	GATTACCCTAGAGCGGCTGG	151-220	14	0.667	0.720	< 0.001	LC655312
Tang29392	ATCACACATTCAGTCAGCGC	GTGTCCATGTCTTCCATTCC	346-350	3	0.389	0.377	ns	LC655313
Tang30982	ACCAAGGACTAGATGCGGAC	GAGGAGGTTTATCGTTGGTG	223-244	7	0.722	0.731	ns	LC655314
Tang33394	ACAGCACCATGAGTTCTGTG	CCGTCGCAATCTACAAGACG	417-425	5	0.676	0.750	ns	LC655315
Tang33405	GATGCCGAACTTCATGCTG	GTTCTTGTCTTGCCTCACG	235-357	22	0.914	0.918	< 0.05	LC655316
Tang33507	ATAATTCATTGCGACCGGGC	GAAGGCAGAAATAGCGGCAC	389-405	9	0.722	0.839	< 0.05	LC655317

N_a, number of alleles; H_o, observed heterozygosity; H_e, expected heterozygosity; HWE, Hardy-Weinberg equilibrium

Table S2. Generalized linear models explaining variation in collector ability

	β	s.e.	Likelihood χ^2	p
Intercept	0.482	1.164	0.16	0.69
Collector A	-0.448	0.377	1.64	0.20
Collector B	0.185	0.171	1.14	0.29
Collector C	-0.147	0.221	0.46	0.50
Collector D	0.794	0.231	9.80	0.0017
Collector E	-0.836	0.295	10.40	0.0013
Collector F	0.039	0.179	0.05	0.83
Collection time	-0.008	0.011	0.53	0.47
Number of collectors	-0.233	0.156	2.02	0.16

Estimated coefficients were used to correct collection effort in 2018 results (Fig. 1).