

1 **Evolution of nuptial gifts and its coevolutionary dynamics with**
2 **"masculine" female traits for multiple mating**

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19 Short title: Trading between male nuptial gifts and female multiple mating

20

21 ABSTRACT

22 Many male animals donate nutritive materials during courtship or mating to their female
23 mates. Donation of large-sized gifts, though costly to prepare, can result in increased
24 sperm transfer during mating and delayed remating of the females, resulting in a higher
25 paternity. Nuptial gifting sometimes causes severe female-female competition for
26 obtaining gifts (i.e., sex-role reversal in mate competition) and female polyandry,
27 changing the intensity of sperm competition and the resultant paternity gains. We built a
28 theoretical model to analyze such coevolutionary feedbacks between nuptial gift size
29 (male trait) and propensity for multiple mating (female trait). Our genetically explicit,
30 individual-based computer simulations demonstrate that a positive correlation between
31 donated gift size and the resultant paternity gain is a requisite for the co-occurrence of
32 large-sized gifts and females' competitive multiple mating for the gifts. When donation
33 of gifts imposes monandry, exaggeration in nuptial gift size also occurs under the
34 assumption that the last male monopolizes paternity. We also analyzed the causes and
35 consequences of the evolution of a female persistence trait in trading of nuptial gifts, that
36 is, double receptacles for nuptial gifts known to occur in an insect group with a "female
37 penis" (*Neotrogla* spp.).

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39

40 *Keywords:* nuptial gift, paternity determination mechanism, coevolution, female

41 persistence trait, female penis, sex role reversal.

42

43 1. INTRODUCTION

44 Nuptial gifts, any non-gametic materials transferred from one sex (usually male) to
45 another during courtship and mating, are widely observed in many groups of animals,
46 such as insects, arachnids, molluscs, amphibians, birds, and mammals including
47 humans (Lewis and South 2012; Lewis et al. 2014). In some cases, male-derived “gifts”
48 can be detrimental to female recipients as the love darts of land snails and anti-aphrodisiac
49 seminal peptides of *Drosophila* fruit flies, both of which mitigate the intensity of sperm
50 competition in female sperm storage organs (Chapman 2001; Chase and Blanchard 2006).
51 However, in many cases, males donate (at least potentially) nutritious materials such as
52 prey items they have collected or voluminous secretions from male internal/external
53 glands (Boggs 1995; Lewis and South 2012).

54 Although this phenomenon is widely observed in the animal kingdom, there is
55 continuing debate on its primary function (Alexander and Borgia 1979; Gwynne 1984;
56 Sakaliuk 1986; Simmons and Parker 1989; Parker and Simmons 1989; Wedell 1993;
57 Wickler 1994; Vahed 1998). Since females of some animals accept mating only while
58 consuming a gift, males may donate the gift to obtain mating opportunities (i.e., mating
59 effort hypothesis). In addition to nourishing female recipients, nutrition from nuptial gifts
60 can be passed to offspring sired by the male donor, and thus can function as paternal

61 investments (i.e., paternal investment hypothesis). Regardless of the ultimate benefits for
62 males, a large nutritious gift is costly for the male to prepare (reviewed in Boggs 1995),
63 although it may be more attractive to females or may enable transfer of more sperm (Sauer
64 et al. 1998; Engqvist et al. 2007; South and Lewis 2012). By improving the nutritional
65 status of female recipients, gigantic nuptial gifts can thus also be a cause of reversal in
66 the sex roles: usually males more actively seek mating opportunities while females are
67 choosier about mates than males, but in sex-role reversed animals, females compete for
68 multiple mating opportunities to obtain more nuptial gifts (Vahed 1998; Gwynne 2008;
69 Fritzsche & Arnqvist 2013; Kamimura and Yoshizawa 2017). Increased polyandry
70 inevitably causes severer sperm competition, changing the cost-benefit balance for males
71 to prepare nuptial gifts. Although several models have been proposed to date for
72 elucidating the evolution of nuptial gifts (Parker and Simmons 1989; Boggs 1990; Alonzo
73 and Pizzati 2010), they did not encompass these possible coevolutionary feedbacks
74 between the sexes for the trading of gifts. The patterns of female sperm storage and use,
75 which determine the benefits in paternity gain of donating a given gift size of gifts, are
76 possible pivotal factors for shaping the coevolutionary dynamics in the trading of nuptial
77 gifts. However, explicit appraisals, both theoretical and empirical, are lacking entirely.

78 To fill this gap, we developed a genetically explicit individual-based model in

79 the present study. For this purpose, we chose *Neotroglia* (Insecta: Psocodea:
80 Prinoglarididae: Sensitibillini) as an illustrative case. A single male ejaculate of *Neotroglia*,
81 which contains voluminous and potentially nutritional seminal substances, forms a
82 gigantic, bottle-shaped capsule (spermatophore) of $\sim 0.05 \text{ mm}^3$, corresponding to $\sim 300 \text{ ml}$
83 if scaled up to human proportions (Yoshizawa et al. 2014, 2018b). Unlike prey items, the
84 size of which cannot be exactly controlled by the male donors, males likely allocate their
85 limited resources for this type of seminal gift to multiple mating opportunities in a
86 strategic manner. This model system provides us the rare opportunity to examine
87 additional complexities in the evolution of sex-role reversed animals, that is, the evolution
88 of “masculine” persistence traits in females for competitively obtaining male-derived
89 gifts. Females of *Neotroglia* use their evolutionarily novel penis-like structure, termed a
90 gynosome, as an intromittent organ for copulation with males. This “female penis” is
91 ornamented with species-specific lobes and/or spine bundles, which are accommodated
92 in specialized pouches of the vagina-like male genitalia during copulation (Yoshizawa et
93 al. 2014). Since they live in dry, nutritionally poor caves in Brazil, the gynosome likely
94 represents an elaborate way for females to exploit seminal gifts from males (Yoshizawa
95 et al. 2014, 2019a). In accordance with this view, females of a related species with similar
96 spermatophores (Psocodea: Trogiidae: *Lepinotus*) compete for access to males (Wearing-

97 Wilde 1995, 1996). Moreover, females of *Neotroglia* and those of related genera of the
98 tribe Sensitibillini (*Afrotroglia* and *Sensitibilla*) have also developed a specialized
99 structure, termed a spermathecal plate, in their sperm storage organ (spermatheca). In
100 *Neotroglia* (and possibly also in *Afrotroglia* and *Sensitibilla*), this evolutionarily novel
101 organ is equipped with twin slots that enable retention and digestion of two seminal gifts
102 simultaneously (Lienhard 2007; Yoshizawa et al. 2014, 2018b, 2019a). By contrast,
103 females of related groups with only a single slot for nuptial gift can accept another mating
104 only after digestion of the content of a spermatophore received at the preceding mating
105 (for example, in *Lepinotus*, Wearing-Wilde 1995). Given that *Neotroglia* females mate
106 multiply as evidenced by up to two full and nine emptied spermatophore capsules in their
107 spermatheca (Yoshizawa et al. 2014), the spermathecal plate of this genus (and probably
108 also of the remaining Sensitibillini) can be considered a female adaptation for obtaining
109 nutritious gifts in rapid succession.

110 In the present study, we examine coevolutionary dynamics between the size
111 (volume) of nutritive seminal gifts, a male trait, and propensity for multiple mating to
112 obtain gifts, a female trait. Resource availability to males, costs of additional mating for
113 females, and the paternity determination patterns in multiply mated females were
114 analyzed as possible factors influencing the coevolutionary dynamics. The evolutionary

115 causes and consequences of females with twin slots for obtaining gifts, hereafter referred
116 to as “2S females”, were also examined in detail to understand the evolution of “masculine”
117 traits in sex-role reversed female animals.

118

119 2. MODEL ASSUMPTIONS

120 All notations and parameter values used in this article are summarized in Table 1. It is
121 likely that a given volume of nuptial gift will increase the female’s fitness more effectively
122 when the female is starving than when she has already received a large amount of
123 nutrients from the preceding mates. Thus, we assumed that the potential offspring number
124 of a female (fecundity, F_{pot}) is a saturation function of the cumulative volume of seminal
125 gifts (r) received in all of her previous matings (Fig. 1):

$$126 \quad F_{pot}(r) = F_{max}(1 - e^{-br}) \quad (\text{eq. 1})$$

127 where b , set at 0.002 throughout the present study, represents the speed of saturation. In
128 this equation, F_{max} , set at 800, denotes the maximum number of offspring that a female
129 can potentially produce when $r = \infty$ under no cost of mating.

130 Even in cases in which males donate nuptial gifts at each mating event, multiple
131 mating, which may involve costly mate-searching and an enhanced risk of being predated,
132 can be detrimental for the females. Thus, we imposed a cost (c) for each mating event, as

133 a reduction in the number of offspring as:

$$134 \quad F(r, c, M_R) = F_{pot}(r) - c \cdot M_R \quad (\text{eq. 2})$$

135 where M_R is the number of performed matings of a focal female.

136 This simple function delineates complicated coevolutionary relationships
137 between the male and female traits (Fig. 1). When males donate a large-sized gift at each
138 mating (e.g., $V = 500$), an additional mating further increases the lifetime fitness of a
139 singly-mated female under a low cost mating (e.g., $c = 100$; orange arrows in Fig. 1), but
140 not when it is largely costly (e.g., $c = 200$; red arrows). From a male perspective, because
141 the fitness gain to a female mate from receiving a unit amount of gift gradually decreases
142 with the total amount of gifts received in previous rounds of mating (r , Fig. 1), preparing
143 small-sized gifts is advantageous because it increases opportunities for mating with
144 females, especially unmated females, who received less or no nutrition from previous
145 matings. However, smaller gifts can result in a higher probability of remating by his
146 female mates when mating cost is sufficiently low. Therefore, males who donate a large-
147 sized gift can enhance the paternity gain by decreasing the probability of remating by
148 their female mates, although the large-sized gift inevitably decreases the number of
149 matings in which that they can engage. Furthermore, in the case that males can transfer
150 more sperm by giving a large-sized gift, it can result in a higher paternity share compared

151 to males who gave a smaller gift to the same mate. Since sperm storage/use patterns of
152 multiply -mated females are largely unknown for animals with donation of nuptial gifts
153 (Lewis and South 2012), we examined four different regimes for the relationship between
154 the nuptial gift size and the resultant paternity gain in this study: (1) perfect correlation
155 (PC), (2) equal shares (ES), (3) complete last male (LM), and (4) complete first male (FS)
156 (Fig. 2, Table 1).

157

158 3. INDIVIDUAL-BASED SIMULATIONS

159 Individual-based evolutionary simulations were conducted to observe the coevolutionary
160 dynamics of three traits: male seminal gift size, female propensity for multiple mating,
161 and the number of slots for obtaining gifts in females. For this, we used personal scripts
162 written in Python 3.7.1, which are available in the Appendix. Simulations were run for
163 2000 generations assuming a single population of diploid organisms. The population size
164 was set at 1000 (500 males and 500 females). Nuptial gift size, a trait of male-specific
165 expression, was assumed to be determined by a set of autosomal polygenes. To mimic
166 sexual reproduction, these polygenes were divided into two groups, one from each parent.
167 The initial genetic value for each polygene group was randomly extracted from a normal
168 distribution, with a mean of 20 and a standard deviation (SD) of 40. Each individual

169 possesses two values, $v1$ and $v2$, as the genotype of this trait. The seminal gift size
170 (volume; V) was determined as the average of these two values only for male individuals
171 as their phenotype. Similarly, a mean of 0.5 ± 2 was given as the initial values for the
172 propensity for multiple mating ($m1$ and $m2$), which determines the maximum number of
173 “additional” matings accepted by each female individual (M), as the nearest integer of
174 $(m1 + m2)/2$. Thus, females of the genotype $m1/m2$ mate $M + 1$ times, whenever a mating
175 opportunity is available. To prevent the occurrence of unreasonable values in these two
176 traits, we set the lower limits of genetic values of these two traits as 20 and 0, respectively.

177 Another female trait, the number of slots for accepting nuptial gifts, was assumed
178 to be a dichotomous trait, that is, one or two slots. Little is known about the evolutionary
179 process of the spermathecal plate, which enables retention of two nuptial gifts
180 simultaneously, in the ancestors of extant Sensitibillini (see Discussion). For simplicity,
181 we assumed that the transition is controlled by a single locus with two alleles: $2s$, a gene
182 for the twin-slot state, and $1s$, a gene for the single-slot state, the former was assumed to
183 be dominant over the latter. The populations were initiated with single-slot females ($1S$,
184 $1s/1s$ homozygotes). Then, $2s$ genes were allowed to invade to populations at 1000th
185 generation and beyond (one spontaneous mutation in each generation), together with
186 recurrent invasion of single-slot mutants (a female individual of $1s/1s$ homozygote per

187 generation) to check the evolutionary stability of the twin-slot state ($2S$). When the $2S$
188 phenotype occupied 95% or more of females, this phenotype was judged as fixed.

189 In the model, each male can mate up to N times, which is R/V rounded up to the
190 nearest integer, where R is a total volume of resource available for production of nuptial
191 gifts, randomly extracted from a normal distribution. The gift size of the last mating (V_{last})
192 is:

$$193 \quad V_{last} = R - (N - 1)V \quad (\text{eq. 3})$$

194 unless R is not a multiple of V .

195 The mean value of R ranged from 400 to 1300, by increments of 100, representing an
196 environmental variability in resource availability. The SD was set at each mean value
197 multiplied by 0.2.

198 In our model, a female accepts additional mating when (1) she has mated fewer
199 times than her acceptable number of matings ($M + 1$), and (2) at least one of her slots is
200 empty. We assumed that in every generation, all virgin females start to mate
201 simultaneously. After the first mating between random male and female pairs, seminal
202 gifts from males were sequentially assigned, one at a time, to the slot that had received
203 the minimum cumulative volume of gifts (r) in the females whose mating demand was
204 not satisfied at the time. This procedure was repeated until all females satisfied their

205 mating demands, or all males exhausted their resource budgets. By this algorithm, we
206 implemented the condition that larger seminal gifts are difficult to digest for females, and
207 thus occupy a slot for a longer duration, resulting in delayed remating of the female.

208 Then, the relative fitness of each female was calculated according to eq. 2. Cost
209 of mating, defined by a reduction in female fitness per mating (Fig. 1), was varied from
210 5 to 95, by increments of 10, and negative fitness values were treated as zero. Maternity
211 and paternity of offspring were determined according to the proportional representation
212 of the relative fitness of females and the relative representation of male sperm in each
213 female (Fig. 2), respectively. For each trait, one of two parental genes was randomly and
214 independently extracted from two parents, and fused to create an individual of the next
215 generation, that is, with no linkage among the three traits. For seminal gift size and
216 propensity for female multiple mating, each of these values was treated as the mean of a
217 normal distribution for creating the genetic values of progenies (recurrent mutation) with
218 SDs 40 or 2, respectively.

219 To dissect the complicated coevolutionary interactions between the male and
220 female traits, simulations were repeated 40 times for each combination of R and c values,
221 and for each of the four different paternity determination regimes (PC, ES, LM, and FM)
222 specified above (Fig. 2). In addition, three different types of simulations were conducted

223 (Table 1). In doubling females (DF) runs, the number of females was doubled, resulting
224 in 1000 females per 500 males, from 1000th generation and beyond, instead of
225 introducing invasion of one twin-slot mutant female (2S female) every generation
226 (doubling slots, DS runs). In the control runs (CON), neither the numbers of slots nor
227 females were doubled throughout the 2000-generation runs. Possible effects of genetic
228 correlation between the male and female traits on their coevolution were also examined
229 (see Supporting Material 2).

230

231 4. RESULTS

232 *Evolution of nuptial gift size and female multiple mating under different paternity-* 233 *determination regimes*

234 Our simulations revealed notable effects of the pattern of paternity determination on the
235 evolution of gigantic seminal gifts and female persistence traits, that is, the propensity for
236 multiple mating and twin slots for obtaining gifts. Under a given set of parameters, the
237 male seminal gift size and female propensity for multiple mating rapidly converged to a
238 respective equilibrium, usually before 300th generation (the left half of Fig. 3 for an
239 example of DS runs; for examples of CON and DF runs, see Supporting Material 1). Only
240 when females used sperm from each male mate for fertilization of eggs proportionally to

241 the nuptial gift size donated (the PC regime) did males evolve a large-sized gift compared
242 with their lifetime resource budget under a wide range of parameter sets (male resource
243 budget [R] and cost of mating for females [c]: Fig. 4A).

244 Under the situations assumed in our simulation, dividing the limited resource (R)
245 into small-sized gifts could increase the mating opportunities of males, while a large-sized
246 nuptial gift could afford males two types of paternity benefits, namely: (1) siring more
247 offspring than males who gave a smaller gift to the same mate; and (2) eliminating the
248 probability of remating by the female as a post-copulatory guard against remating.
249 Because the former type of benefit occurs only under the assumption of the PC regime,
250 this can explain the observed prevalence of the “fewer large” strategy over “many small”
251 in this regime. Accordingly, females evolve the propensity to mate multiply for these
252 attractive, large-sized gifts when available, but males generally cannot satisfy the inflated
253 females’ demands (Figs. 4A, 5A). Exceptions are when the mating cost is extremely large
254 (high c) and the environment is eutrophic (high R , the upper-right corners of Figs. 4A and
255 5A). The former condition lowers the attractiveness of a given size of gifts, making a
256 single mating almost optimal for females. The latter condition can shift male strategies to
257 “many small” for seeking many virgin females, rendering their gifts more unattractive to
258 females.

259 When the paternity was equally assigned to all mates of a female (ES), males
260 generally did not evolve a large-sized nuptial gift (Fig. 4B). As discussed above, this can
261 be attributed to the lack of paternity benefits proportional to the donated gift size in this
262 regime. To collect these small gifts from many males, females mated more frequently
263 than under the PC regime, especially when mating cost was low and the habitat was
264 eutrophic (Fig. 4B). By behavioral modulation, females usually accomplished their
265 required number of matings (Fig. 5B). An exception is the condition with very small
266 mating costs and oligotrophic environments (the lower-left corners of Fig. 4B), where
267 additional mating is always beneficial even for small-sized gifts.

268 Under the assumption that the first male monopolizes the resultant paternity
269 (FM), males are expected to increase their opportunities to be the first mate of females by
270 reducing the size of each gift. Interestingly, the resultant coevolutionary patterns of the
271 nuptial gift size and the female persistence traits were almost identical between the ES
272 and FM regimes (Figs. 4D, 5D), indicating that sexual selection works quite similarly in
273 these two regimes.

274 When the last male monopolized the paternity (LM), males generally evolved
275 larger-sized gifts compared to the FM and ES regimes (Fig. 4C). To be the last mate, we
276 can envisage two different strategies: preparing many small gifts increases the

277 opportunities for being the last mate by chance (as in the FM and ES regimes), while
278 provision of a large-sized gift is advantageous because it reduces the probability of
279 remating by the female. The latter strategy must be especially effective when females tend
280 to seek additional mating opportunities because of low mating cost. Thus, the observed
281 large gifts when c is low (the lower areas of Fig. 4C) can be a countermeasure of males
282 for preventing frequent remating of their mates. When mating is more costly for females,
283 it is less necessary for males to prepare large gifts, and this prudence itself reinforces the
284 females' reluctance for further mating. Accordingly, for high c values, females satisfied
285 their mating demands when the habitat was eutrophic (high R , Fig. 5C). An important
286 exception is the extremely oligotrophic environments ($R = 400$) with extremely high cost
287 of mating ($c = 85-95$) (the upper-left corners of Figs. 4 and 5). Under this combination
288 of parameters, males also evolve comparatively larger gifts under the ES and FM regimes,
289 even though it does not result in overly high mating demands of females that males cannot
290 satisfy. Given extremely high mating costs for females, males experience a low risk of
291 sperm competition. In addition, if males have extremely limited resources for preparing
292 gifts, premating male-male competition should be also less severe. Accordingly, males
293 likely shift toward providing the monandrous female as much as their resource budget
294 allows.

295 In our simulation, the genetic correlation between seminal gift size ($([v1 + v2] /$
296 2) and female mating propensity ($([m1 + m2] / 2)$) was negligibly low (near zero), and thus
297 elimination of genetic covariance by shuffling paternal identity did not change the results
298 (Supporting Material 2).

299

300 *The evolution of twin-slots and its effects on the coevolutionary processes*

301 Figure 5 clearly shows that 2S females successfully invaded into a population when
302 females could not satisfy their required number of matings on average (Fig. 5). Such a
303 condition occurs (1) when mating costs for females are extremely low and the
304 environment is oligotrophic regardless of the paternity determination regimes, or (2)
305 when males evolve large-sized gifts, reception of which is beneficial for females and
306 outweighs the associated mating costs. Males evolved such an “effective” gift for making
307 females monandrous (under the LM regime, Fig. 4C), or for siring more offspring of
308 multiply mated females (under the PC regime, Fig. 4A).

309 Under these conditions, 2s genes for making the twin slots usually increased
310 rapidly and became fixed in the population (Fig. 3). Prevalence of 2S females caused a
311 coevolutionary reduction in male gift size (Fig. 3). Accordingly, females needed an
312 increased number of matings to approach their fitness optimal, resulting in a reduction in

313 their average fitness (Fig. 6B). When mating cost was relatively low, females could not
314 satisfy their demands even with an increase in mating frequency by possessing two slots.
315 However, with a higher mating cost and especially in eutrophic habitats, the smaller sized
316 gifts, as a male counter-adaptation to twin slots, became unattractive to the females,
317 resulting in a higher satisfaction rate (compare Fig.5A-c with 5A-b).

318 Strikingly similar patterns were observed when the number of females was
319 doubled at the middle of simulation runs (Fig. 6A; Supporting Material 1). However,
320 under each parameter set, the observed reduction in fitness was less prominent when 2S
321 females were fixed compared to when the female number was doubled (Fig. 6B), while
322 among-individual variations in female fitness (measured as SDs) were comparative, being
323 higher than the controls (Fig. 6C).

324

325 5. DISCUSSION

326 *Coevolutionary dynamics for trading nuptial gifts*

327 This study demonstrated notable effects of ecological factors on the coevolutionary
328 feedbacks among seminal gift size, female propensity for multiple mating, and twin slots
329 for obtaining gifts. When mating costs for females are extremely low in oligotrophic
330 environments, females compete for male derived nutrients regardless of the paternity

331 determination regimes. This result supports the view that scarcity of other nutritive
332 sources for female reproduction can be a favorable factor for the evolution of high
333 dependency on male-derived gifts (Gwynne 2008; South et al. 2010). The paternity-
334 determination regimes also show complicated interactions with these ecological factors
335 in determining the coevolutionary feedbacks. Except for when the mating costs are
336 negligibly low in extremely oligotrophic habitats as discussed above, both female traits,
337 high mating rates and twin-slots, rarely evolved in the ES and FM regimes. In addition,
338 in the LM regime, males evolved gigantic gifts almost exclusively when their donation
339 imposed monandry of the females. A strong positive correlation between male seminal
340 expenditure and the resultant paternity is a requisite for the evolution of effective nuptial
341 gifts coupled with female polyandry for obtaining the gifts under a wide variety of
342 environmental variables (Fig. 5).

343 There are only a few preceding studies on the coevolutionary feedbacks between
344 the sexes in trading of ejaculate components. Like nutritious materials in nuptial gifts,
345 sperm itself can be considered as a limited resource for both sexes (Dewsbury 1982;
346 Nakatsuru and Kramer 1982; Olsson et al. 1997; Wedell et al. 2002; Damiens and Boivin
347 2006; Bro-Jørgensen 2007; Reinhardt et al. 2011; Abe 2019). Considering a situation
348 equivalent to the PC regime of this study, a previous study examined the effects of several

349 environmental factors on the evolutionary feedbacks between male sperm allocation
350 strategies and female mating rate (Abe and Kamimura 2015). In the model, increased
351 mating costs for females (c_f , equivalent to our c) resulted in a lower female mating rate
352 and an increased sperm package size, similar to the results of the present study. The
353 study also showed that reduction in resource availability to males (low R) results in a
354 monotonic reduction in the ejaculate size (Abe and Kamimura 2015). Although our
355 present model showed similar dependency of seminal gift size (V) to R , prudently
356 allocated gifts were also observed in extremely eutrophic environments with high female
357 mating costs (Fig. 4A). This difference can be attributed to the different assumptions
358 adopted: in the model of Abe and Kamimura (2015), males suffer a reduced mating rate
359 only when females experience a shortage of sperm supply. This condition hampers the
360 evolution of “many small” strategies when females are almost monandrous just to avoid
361 high mating costs, while males have sufficient resources for making many seminal
362 packages.

363 Bocedi and Reid (2016) also examined the effects of varying female mating costs
364 on the coevolutionary feedbacks between male sperm traits (sperm number and sperm
365 longevity) and female mating frequency. Under “fair raffle” sperm competition
366 (equivalent to our PC regime), an increase in female mating costs resulted in reduced

367 polyandry, as seen in the present study, but also in a reduction of sperm number
368 transferred during a single mating event. The latter finding makes a striking contrast to
369 our results in which males prepare larger gifts for less polyandrous females unless the
370 environment is not extremely eutrophic (Fig. 4A). This can also be attributed to the
371 different assumptions adopted for trade-off relationships: the model of Bocedi and Reid
372 (2016) “does not explicitly consider any precopulatory male traits; overall mating
373 frequencies are primarily determined by female mating rate,” indicating no size-number
374 trade-offs. Instead, males increase the sperm number at a cost of reduced sperm longevity
375 in their model, where males should invest more resources to sperm longevity when they
376 experience a low sperm competition risk.

377 By modulating a “raffle loading factor,” Bocedi and Reid (2016) also found that,
378 when the first or last males have an advantage in fertilization success (nearly equivalent
379 to our FM or LM regimes), females tend to be more polyandrous, similar to our results.
380 However, again, different mechanisms likely underlie these superficially similar results.
381 Under the assumption of the number-longevity trade-off in sperm considered by Bocedi
382 and Reid (2016), males invest less in sperm number when the first males have advantages
383 for the sake of enhanced sperm longevity in the female sperm storage. By contrast, under
384 the assumption of last-male sperm precedence, polyandrous mating is likely reinforced to

385 compensate for high fertilization failure caused by reduced sperm longevity, though males
386 provide a large number of sperm per mating (Bocedi and Reid 2016).

387

388 *Relevance to empirical studies*

389 There is ongoing debate on the primary function of nuptial gifts for male donors, as they
390 may function as mating efforts or paternal investments for their offspring (see
391 Introduction). Recent studies suggest that these two hypotheses are not mutually
392 exclusive and are difficult to discriminate, because male-derived nutrients cannot be
393 properly allocated to the offspring of respective donors without a positive correlation
394 between the extent of mating efforts by males and their paternity success (Lewis and
395 South 2012). The results of the present study provide important insights for the difficulty
396 in discriminating these two hypotheses. Nutritious nuptial gifts are effective as male
397 mating efforts when females compete to accept (additional) mating to obtain them. The
398 present study revealed that such effective nuptial gifts evolve almost exclusively when
399 donation of large-sized gifts results in high paternity gains, measured as the number of
400 offspring nourished by the female (the PC or LM regime).

401 Vahed (2006) explored relationships between degree of polyandry and nuptial
402 gift size among bushcricket species. He found that nuptial gift size (spermatophylax

403 volume) is not correlated with the degree of polyandry. However, gift size relative to body
404 size tended to be large in species with large seminal components with possible anti-
405 aphrodisiac effects. Thus, larger gifts may have been evolved to overcome female
406 refractory behavior. This additional complexity was not considered in the present model.

407 To keep our model simple, we did not incorporate the following factors that
408 likely affect trading of nuptial gifts: assessment of gift size by females before receiving
409 the gift, strategic modulation of gift size by males based on mating status of mates (e.g.,
410 unmated vs. previously mated females), and costs of mating itself for males. For
411 *Neotrogla* spp. in which copulation with the female positioned above the male lasts for a
412 long period (41–73 hours in *N. curvata*, Yoshizawa et al. 2014), the last factor can be
413 especially relevant.

414 We also assumed only a single reproductive output at the end of the female life
415 (semelparity). However, in iteroparous species with multiple reproductive bouts, a male
416 may monopolize paternity in each bout by donating a large gift, even in the cases that
417 females are polyandrous through their life. In addition, seminal gift size can also vary
418 interspecifically through possible macro-evolutionary trade-offs with other male and
419 female traits: male calling frequency in bushcrickets (Del Castillo and Gwynne 2007),
420 male weaponry in megalopteran insects (Liu et al. 2015), and male bioluminescent

421 courtship and female flightlessness in fireflies (Lewis and Cratsley 2008; South et al.
422 2011; South and Lewis 2012). These complexities should be taken into account when
423 comparing theoretical predictions with empirical data.

424

425 ***Why did a “female penis” evolve in Sensitibillini***

426 There are several hypothetical factors that have promoted the evolution of a “female penis”
427 in *Neotrogla* (Yoshizawa et al. 2019a). In Sensitibillini, a tribe of the family
428 Prinoglarididae with only eleven named species in the three genera known to date,
429 females of *Afrotrogla* also possess a well-developed, presumably protrudable penis, while
430 the homologous part forms only a small projection in the sister genus *Sensitibilla*
431 (Lienhard 2000, 2007; Lienhard et al. 2010b). Although its function has not yet been
432 determined, the morphology of the *Afrotrogla* female penis differs significantly from
433 those of *Neotrogla* (Lienhard 2007, Lienhard et al. 2010a, Yoshizawa et al. 2018a). Thus,
434 a female penis with an intromittent function is considered to have evolved twice
435 independently in this small insect tribe (Yoshizawa et al. 2018a).

436 Like all other members of the tribe Sensitibillini known to date, *Neotrogla* spp.
437 exclusively occur in oligotrophic, dry cave habitats (Lienhard et al. 2010a, Lienhard and
438 Ferreira, 2013). In addition, they retain ancestral female-above mating positions (Fig. 2),

439 suggesting that males do not impose high mating costs to females. Our present study
440 demonstrates that under these conditions, that is, low R plus low c , males likely evolve
441 large-sized gifts, for which females compete to acquire, regardless of sperm usage
442 patterns. As in many other animals with nuptial gifts, sperm usage/storage patterns are
443 completely unknown at present for the members of *Neotroglia*. However, the males
444 provide considerably large gifts to polyandrous females, as evidenced by multiple
445 emptied spermatophore capsules in the female spermatheca (Yoshizawa et al. 2014). It is
446 also true for *Lepinotus* (Trogidae) (Spratt 1989), females of which have only a single slot
447 for digesting nuptial gifts (Wearing-Wilde 1995). Thus, the PC regime, in which co-
448 occurrence of large-sized gifts and polyandry is prevalent, is the most plausible for this
449 group of insects. Since many psocids show continuous production and deposition of eggs
450 after sexual maturity (Söfner 1941; New 1987), the LM regime is also a candidate if
451 females mate with a single male in each oviposition interval.

452 Interestingly, among Psocodea (booklice, barklice, and parasitic lice), the
453 spermathecal duct (sperm corridor) is comparatively long and narrow in Trogiomorpha,
454 in which formation of gigantic spermatophores is the norm, and is especially elongated
455 and coiled in Sensitibillini (Klier 1956; Lienhard 1998, 2000; Lienhard and Ferreira 2013;
456 Yoshizawa et al. 2019a). In the hangingfly *Hylobittacus apicalis* (Mecoptera: Bittacidae),

457 females accept mating only while eating a nuptial gift (small arthropod prey) donated by
458 the male. Their narrow and elongated spermathecal duct disturbs rapid sperm transfer
459 from males. Therefore, only males who offer a large prey item are allowed to transfer
460 enough sperm to assure their paternity (Thornhill 1976). In other words, if a spermathecal
461 duct is wide and short, enabling rapid transfer of sperm, males may easily evolve a
462 cheating strategy such that they pass a large number of spermatozoa with a minimal
463 nuptial gift (see Hayashi 1999 for possible examples in megalopteran insects). Thus, it is
464 highly plausible that the narrow and extremely long sperm corridor of Sensitibillini has a
465 function similar to those of hangingflies, as a cryptic female choice mechanism for
466 enabling a positive correlation between seminal gift size and transferred sperm number.

467 The results of the present study support the view that the evolution of twin slots
468 can also be a crucial factor favoring the evolution of a manipulative intromittent organ in
469 the female, as it can reinforce female-female competition for male-derived nutrients (see
470 below). Despite the astonishing diversity in their morphology, our knowledge on the
471 reproductive biology of the order Psocodea is quite limited. For example, although some
472 *Neotrogla* females possess two freshly deposited spermatophores attached to the twin-
473 slots (Yoshizawa et al. 2014), it is presently unknown whether they are derived from two
474 different males. Future studies should also clarify the nutritional effects of

475 spermatophores and sperm usage patterns in this unique group of insects.

476

477 *Coevolutionary feedbacks results in sex-role reversals*

478 Our simulations demonstrated that twin slots for obtaining gifts in rapid succession are
479 advantageous when females cannot achieve their required number of matings, and that
480 the evolution of this persistence trait has notable effects on the coevolutionary dynamics
481 in trading of nuptial gifts between the sexes. Little is known about the transitional process
482 from the single-slot state, which certainly is ancestral in psocids, to the twin slots
483 observed uniquely in Sensitibillini in the animal kingdom. The twin-slots state is
484 estimated to have emerged from 177.5 Mya (95% confidence interval: 103.2–265.3 Mya)
485 to 127.2 Mya (68.7.2–200.8 Mya) in a common ancestor of the extant Sensitibillini, in
486 arid or semi-arid zones of the Pangea or Gondwana supercontinent (Yoshizawa et al.
487 2019b). Since the spermathecal plate of the extant Sensitibillini is a complex structure
488 harboring not only the twin slots for seminal gifts, but also a muscle-driven mechanism
489 to switch seminal flows between them (Yoshizawa et al. 2018b), it has likely evolved
490 gradually from primitive precursors during its long evolutionary history of approximately
491 50 million years. Although we assumed that single-slot and twin-slots states can be
492 switched by two alleles of a single locus, many associated genes must have been modified

493 to create this evolutionarily novel structure. Future studies on the developmental
494 processes of the spermathecal plate and their underlying genes will help us understand
495 the difficulties of the evolution of this complex structure.

496 Abe and Kamimura (2015) have demonstrated that when the sex ratio is strongly
497 biased toward females, males prepare smaller ejaculates for mating with more females.
498 Therefore, the observed effects of the evolution of twin slots is directly comparative to
499 those of female-biased sex ratios. However, unlike doubling the female number, the
500 evolution of twin slots usually resulted in less pronounced reduction in female fitness
501 with its comparatively large variance (Fig. 6). A larger variation in the female fitness
502 means stronger sexual selection operating among them.

503 Male persistence traits, such as genital spines for anchoring unwilling mates or
504 intromittent organs for traumatic insemination, can reduce the total fitness of their mates
505 (Reinhardt et al. 2014; Tatarneck et al. 2014). Theoretical studies show that this kind of
506 inconsistency between male and female interests can even result in a high risk of
507 extinction, driven by the evolution of male “selfish” traits for escalated male-male
508 competition for mates (Rankin et. al., 2011). This type of trait can also be exaggerated
509 through arms races between the sexes so that females also develop counter-adaptations to
510 resist or tolerate male persistence (sexually antagonistic coevolution; e.g., Brennan and

511 Prum. 2014). There are two possible causes for the observed reduction in the average
512 female fitness followed by the spread of 2S females. First, twin slots themselves can
513 directly inflate the among-female variation in cumulative amount of nutrients (r), and
514 thus can reduce the average fitness under the assumption of a saturating fitness function
515 (Fig. 1). Second, as a coevolutionary response for filling the increased number of slots,
516 males reduce the size of each gift, resulting in an increase in the optimal number of
517 matings for females. These lines of findings indicate that even “persistence” traits can be
518 in the category of sex-reversed traits, driven by the evolution of effective nuptial gifts.
519

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651

652 FIGURE LEGENDS

653 Fig. 1 Female fecundity as a saturating function of seminal nutrients from males. See eqs.

654 (1) and (2) in the main text. When males provide a seminal gift of size 500 ($V =$

655 500), females that mated once should seek another mating opportunity when the

656 cost of mating is low (orange arrows, $c = 100$), but not under a higher cost (red

657 arrows, $c = 200$).

658 Fig. 2 A scheme of four different regimes of the relationships between seminal gift size

659 and the resultant paternity. Note that *Neotroglia* shows a female-above mating

660 posture similar to many other species of Psocodea.

661 Fig. 3 **(a)** An example of the coevolutionary dynamics observed between the male seminal

662 gift size (V , blue) and the optimal number of matings for females (M_o , red), together

663 with changes in the realized number of matings by females (M_R , orange) and female

664 fitness (F , green). **(b)** Changes in the proportion of females with twin slots ($2S$),

665 which started to invade the population at the 1000th generation (the black

666 arrowhead), with schematics of $1S$ and $2S$ states. Solid lines and shaded areas of

667 respective lighter colors show the mean \pm SD for 40 runs under the PC regime ($R =$

668 800, $c = 55$).

669 Fig. 4 Average male seminal gift size (V , light blue backgrounds) and the realized number

670 of matings by females (M_R , pink backgrounds) at the 2000th generation observed in
671 the control runs (CON) of four different paternity-determination regimes (**A**, PC; **B**,
672 ES; **C**, LM; and **D**, FM).

673 Fig. 5. Average satisfaction rate (M_R/M_O) of female mating demands in CON (**a**) and DS
674 (**c**) runs, and proportion of 2S females (**b**) in DS runs at the 2000th generation (**A**,
675 PC; **B**, ES; **C**, LM; and **D**, FM). The asterisks in **A-a** indicate the parameter sets
676 examined in **Fig. 6**.

677 Fig. 6. Box plots of the average female fitness (**a**), SD of female fitness (**b**), and average
678 male gift size (**c**) observed at the 2000th generation under the PC regime. Results
679 for four different parameter sets, indicated by the asterisks in **Fig.5A-a** and the three
680 different simulation modes (CON, control; DS, twin-slots invasion; DF, doubled
681 number of females) are shown.

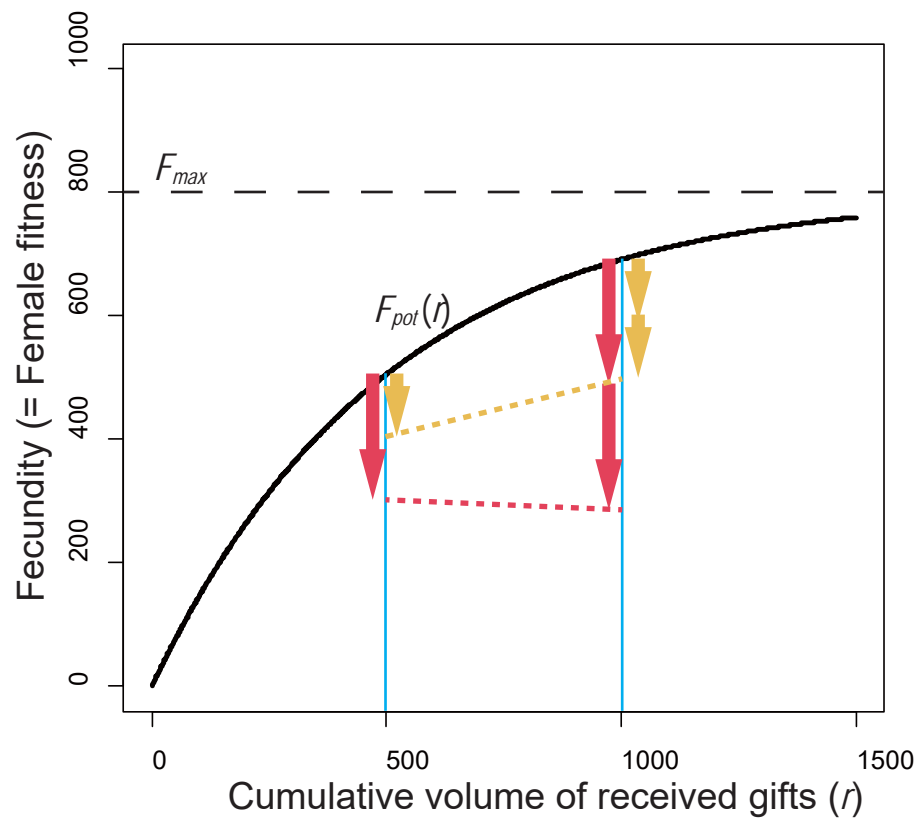


Fig. 1

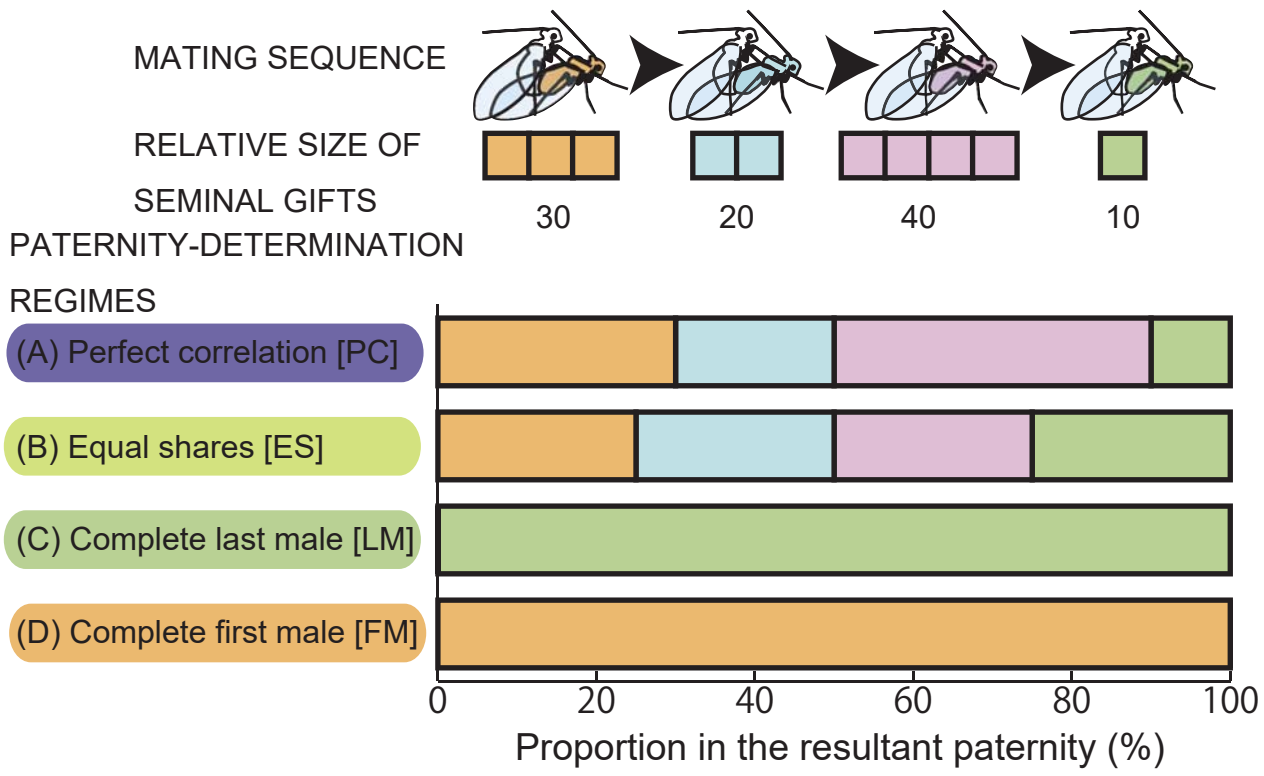


Fig. 2

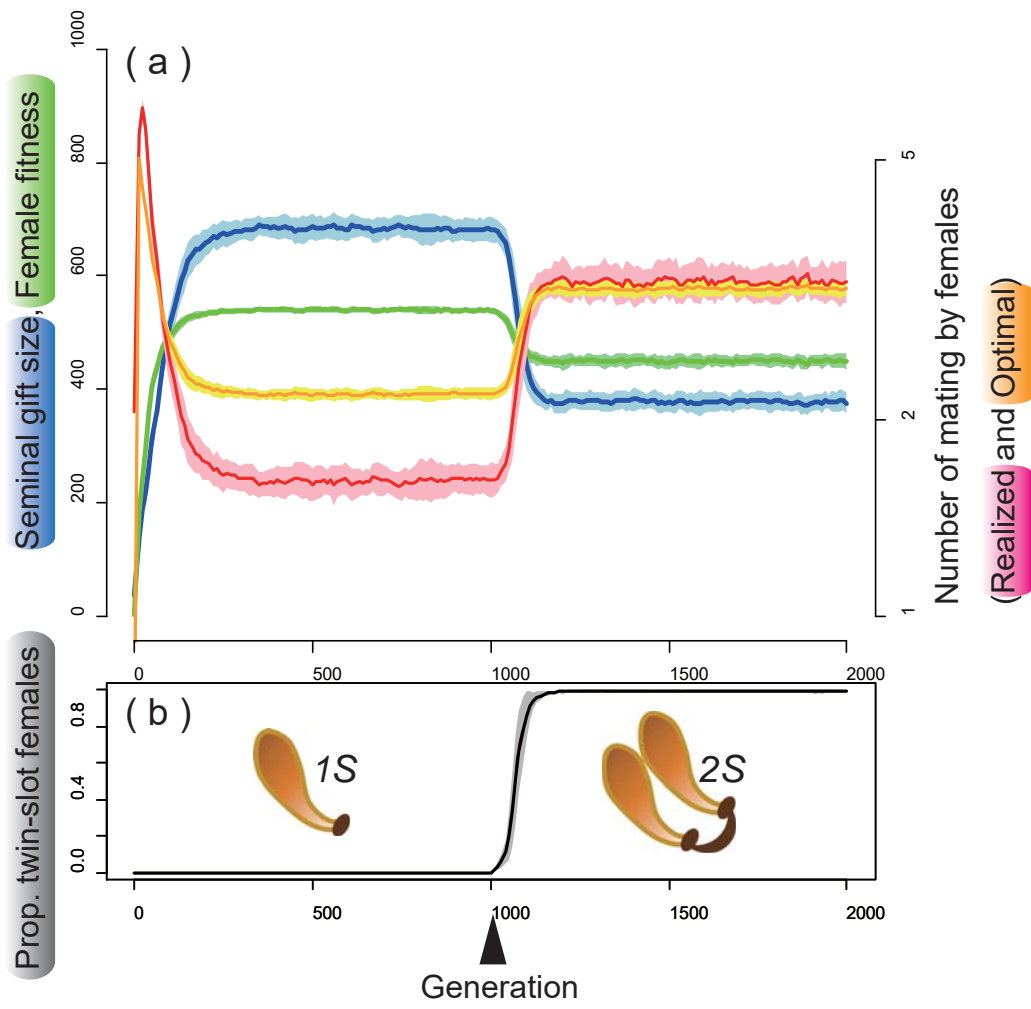


Fig. 3

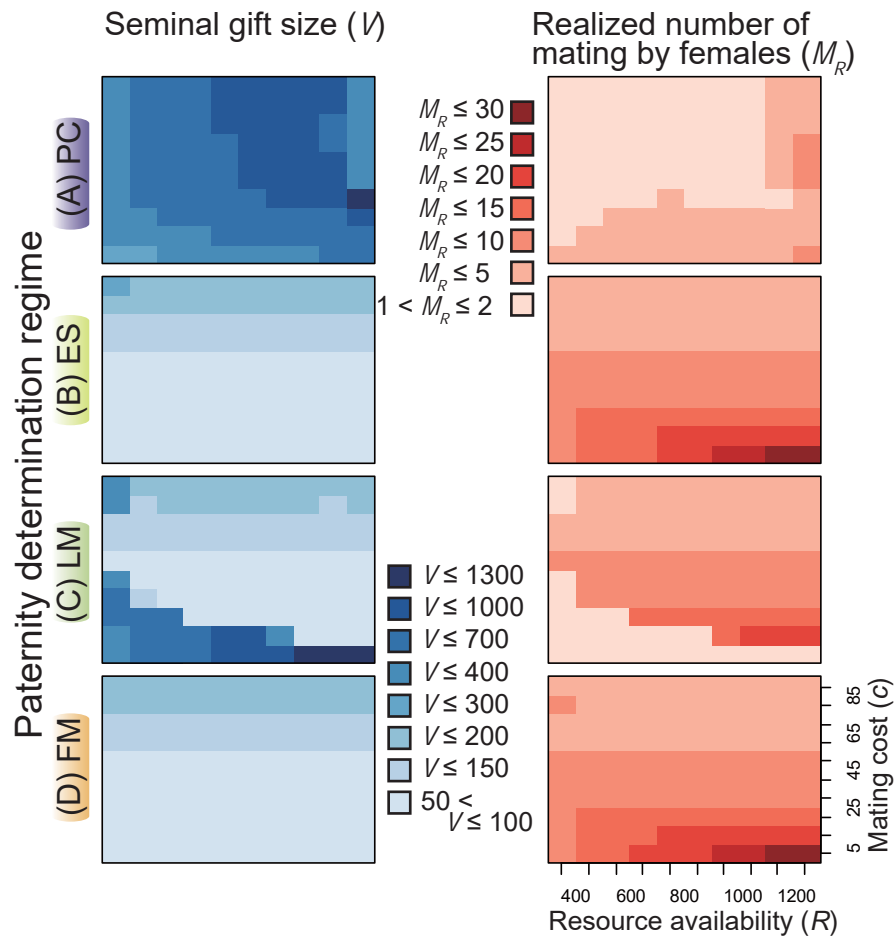


Fig. 4

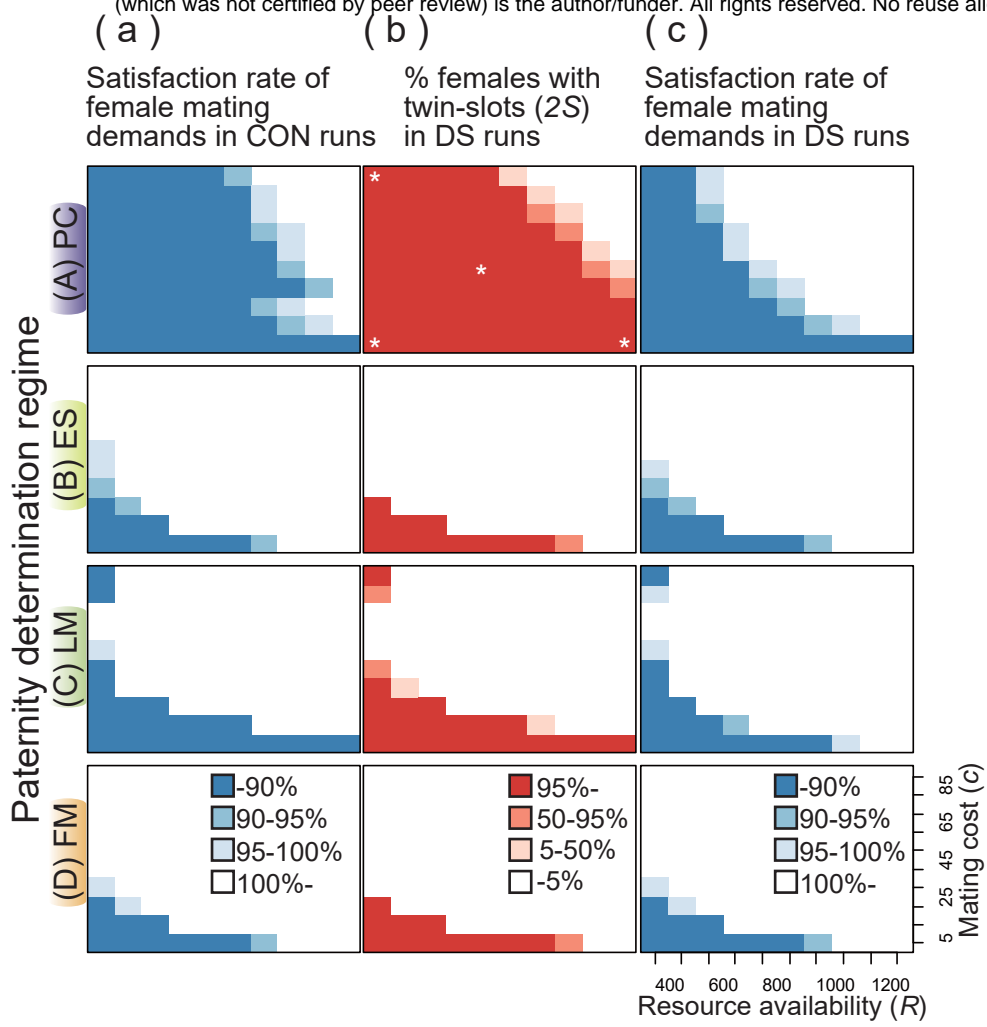


Fig. 5

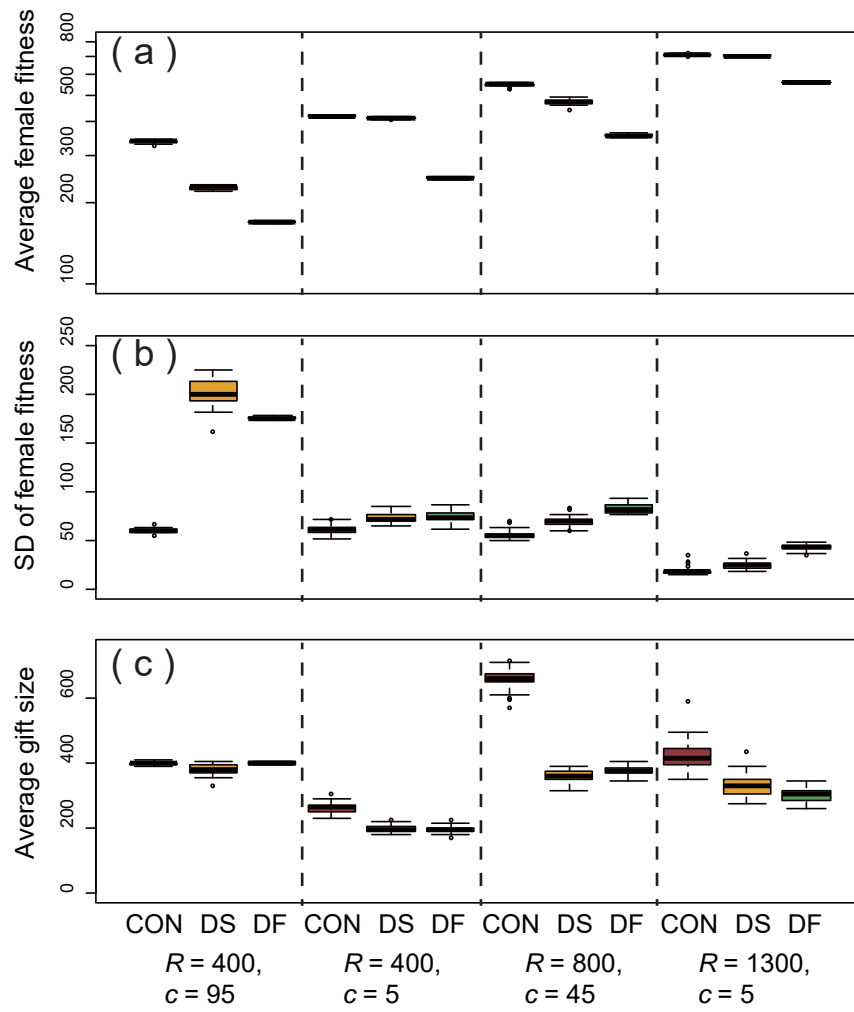


Fig. 6

Table 1. Summary of notation and abbreviations used in this study.

Symbol	Definition and designated values
MODEL PARAMETERS	
$v1, v2$	Genetical values of male seminal gift size from male and female parents, respectively. Initial values were given as a normal distribution (mean \pm SD = 20 ± 40) with truncation (≥ 20).
V	Phenotypic value of male seminal gift size, calculated as $(v1 + v2)/2$.
V_{last}	Seminal volume of the last mating of a focal male, given as eq. 3
$m1, m2$	Genetical values of female acceptable number of mating from male and female parents, respectively. Initial values were given as a normal distribution (mean \pm SD = 0.5 ± 2) with truncation (≥ 0).
M	Phenotypic value of female acceptable number of additional mating (= propensity for multiple mating), calculated as $(m1 + m2)/2$.
M_R	Realized number of mating by females
M_O	Optimal number of mating by females calculated by solving eq. 2
$2s$	Dominant gene for producing twin slots for receiving gifts
$1s$	Recessive gene for producing a single slot for receiving gifts
$2S$	Females of the genotype $2s/2s$ or $2s/1s$, having twin slots for insemination
$1S$	Females of the genotype $1s/1s$, having a single slot for insemination
R	Average total volume of resource for producing seminal gifts, ranged 400-1300 by an increment of 100 depending on the resource availability of the habitat. Each male has a resource budget extracted from a truncated normal distribution mean \pm SD = $R \pm 0.2R$ (> 0).
N	Possible number of mating for a focal male, given as R/V , rounded up to the nearest integer.
r	Cummulative volume of gifts received by a female
b	Fertilization efficiency (this parameter represents the saturating speed of female reproductive output). Treated as a constant ($b = 0.002$) in this study.
F_{max}	Maximum female reproductive output (e.g., offspring number of a female when $r = \infty$ and $c = 0$). Treated as a constant ($F_{max} = 800$) in this study.
c	Mating cost for females, ranged 5-95 by an increment of 10
$F_{pot}(r)$	Maximum fecundity of a female, as a function of b, k and r , before reduction by mating costs
$F(r, c, M_R)$	Realized fecundity of a female, as a function of b, k, r, M_R , and c .
PATERNITY DETERMINATION REGIMES	
PC	Paternity is perfectly correlated with the relative gift size
ES	Paternity is equally shared by all male mates
LM	The last male monopolizes paternity
FM	The first male monopolizes paternity
SIMULATION MODES	
CON	The control simulation runs with neither invasion of $2S$ females nor doubling in female number
DS	One $2S$ female per generation was introduced from 1000th generation and beyond
DF	The number of females were doubled at 1000th generation (i.e., 1000 females for 500 males)