

1 Genomic imprinting drives eusociality

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24 **Abstract**

25 The origin of eusociality, altruistically foregoing personal reproduction to help others, has
26 been a long-standing paradox ever since Darwin. Most eusocial insects and rodents
27 likely evolved from subsocial precursors, in which older offspring “helpers” contribute to
28 the development of younger siblings without a permanent sterile caste. The driving
29 mechanism for the transition from subsociality (with helpers) to eusociality (with lifelong
30 sterile workers) remains an enigma because individuals in subsocial groups are subject
31 to direct natural selection rather than kin selection. Our genomic imprinting theory
32 demonstrates that natural selection generates eusociality in subsocial groups when
33 parental reproductive capacity is linked to a delay in the sexual development of offspring
34 due to sex-antagonistic action of transgenerational epigenetic marks. Focusing on
35 termites, our theory provides the missing evolutionary link to explain the evolution of
36 eusociality from their subsocial wood-feeding cockroach ancestors, and provides a novel
37 framework for understanding the origin of eusociality.

38

39 **Introduction**

40 The origin of eusociality poses a major challenge to Darwin's theory of natural selection
41 (Darwin, 1859) and it remains a subject of debate today (Kay et al., 2020; Nowak et al.,
42 2010; Wilson and Hölldobler, 2005). Eusociality is an advanced state of sociality
43 characterized by the presence of workers that forego personal reproduction in exchange
44 for altruistic behavior toward close relatives. It has long been studied within the paradigm
45 of inclusive fitness and kin selection (Hamilton, 1964). However, the role of kin selection
46 in the origin of eusociality remains controversial (Wilson and Hölldobler, 2005).
47 Explanations of the origin of new traits are faced with the “selection paradox,” the notion
48 that selection cannot act on traits that do not yet exist, and therefore cannot directly
49 cause novelty (Jacob, 1977; Müller and Wagner, 1991). While biologists have made
50 great progress in the last 150 years in understanding how existing traits diversify, we
51 have made less progress in understanding how novel traits arise in the first place. What
52 generates the novelty—here the first appearance of sterile workers?

53 In colonies of eusocial insect (ants, bees, wasps and termites), workers take on non-
54 reproductive tasks and contribute to their parents' reproduction (Wilson, 1971). The
55 colony essentially behaves as a superorganism operating as a functionally integrated

56 unit, analogous to the organization of unitary organisms (Hölldobler and Wilson, 2009).
57 In eusocial colonies, the worker caste is an extended phenotype of the parents. Unlike
58 unitary organisms, however, the extended phenotype of a social insect colony enables
59 selection to act at both the individual (within-colony selection) and colony levels
60 (between colony selection). Suppose the first eusocial colony appears on Earth. This
61 colony uniquely has lifelong sterile workers, while all other attributes are identical to
62 other colonies. Initially, the colony cannot compensate for the loss of fitness due to
63 sterility of some offspring unless the parents can simultaneously increase their
64 reproductive output to produce a greater number of fertile offspring. One or more
65 underlying mechanisms are required to link worker sterility with increased reproductive
66 capacity of the parents.

67 Termite societies, like those of eusocial Hymenoptera (ants and some bees and
68 wasps), are generally large families with a reproductive division of labor. These two
69 groups evolved complex societies independently with different life history pre-
70 adaptations for social evolution. Termites are the oldest social insects, with societies
71 dating back to 150 million years ago (Bourguignon et al., 2015). Eusociality in termites
72 evolved from a subsocial precursor that lived in close family groups and occupied dead
73 trees, as in its sister group Cryptocercidae (woodroaches) (Thorne, 1997) (Fig. 1). The
74 confined nest cavities, slow development due to poor nutritional quality of wood, and
75 need for refaunation of obligate gut symbionts selected for parental care and long-term
76 associations of monogamous family groups (Nalepa, 1994). One requisite condition for
77 the origin of eusociality is iteroparity, which is not present in extant semelparous
78 woodroaches (Korb, 2008; Thorne, 1997). In the subsocial ancestor, iteroparous parents
79 produced brood of staggered age classes living together, where all surviving offspring
80 eventually matured into reproductive imagoes and dispersed to found new colonies.

81 The evolutionary transition from subsociality to eusociality, where the older brood
82 spend a prolonged period in the immature stages within the natal nest and eventually
83 become lifelong workers that contribute to the production of younger brood, is an enigma
84 (Korb, 2008; Thorne, 1997). Although the shift of brood care from parents to older
85 offspring, i.e., helpers, allows the parents to engage more in reproduction, selection is
86 still acting at the individual level rather than the colony level at the subsocial stage. Why
87 did helpers delay and eventually sacrifice their own reproduction under individual-level
88 selection? We show that this paradox can be solved by genomic imprinting.

89 Recent studies reveal that the transfer of epigenetic marks from parents to offspring
90 can influence offspring phenotype independently of DNA sequence (Bonduriansky and
91 Day, 2008; Chong and Whitelaw, 2004; Ferguson-Smith, 2011; Jablonka and Raz,
92 2009). Such ‘epigenetic inheritance’ provides the key to many unsolved puzzles in a
93 wide range of biological processes by circumventing the limitations of genetic inheritance
94 (Bonduriansky and Day, 2008; Matsuura, 2020a; Pál and Miklós, 1999). Genomic
95 imprinting can be differentially marked in eggs and sperm, and inheritance of these
96 epigenetic marks causes genes to be expressed in a parental-origin-specific manner in
97 the offspring (Reik and Walter, 2001). Genomic imprinting has been proposed as a
98 mechanism underlying the parental effects on caste determination (Matsuura et al.,
99 2018) and the evolution of asexual queen succession in termites (Matsuura, 2017;
100 Matsuura et al., 2018, 2009) (see supplementary text, Figs. S1 and S2). Thus, queen-
101 and king- specific epigenetic marks antagonistically influence the development of
102 offspring resulting in “neuter” workers whose sexual development is suppressed due to
103 counterbalanced maternal and paternal imprinting.

104

105

106 **Model**

107 **General framework.** To consider the evolutionary transition from subsocial to eusocial
108 in the ancestor of termites, we suppose a diploid subsocial organism in which a male
109 and a female cooperatively found a new colony in an enclosed habitat. We performed
110 evolutionary simulations by running colony generation G , where each generation
111 includes a colony life cycle as a part of the simulation (Fig. 2, Fig. S6). The colony life
112 cycle is given as follows. An individual has longevity Φ (years), where its age i varies
113 from 0 to Φ . Individuals spend τ ($\geq \tau_{min}$: the shortest time to become alates) in their
114 natal nests and become alates that disperse. The colony dies when the parents die.
115 Thus, colony longevity T is given by $\Phi - \tau$ (Fig. 2A), where colony age t varies from 0 to
116 T . Fitness gain ω_t of the colony at t is the sum of the reproductive values of dispersing
117 alates (Fig. 2A). Total fitness of the colony W is given by

$$118 \quad W = \sum_{t=0}^T \omega_t .$$

119

120 **Colony foundation.** We consider a monogamous pair of a male and a female founding
121 a new colony in a nest inside wood. The work performance of each parent is ρ (J/year),

122 that is, the amount of resources acquired by a parent. Both the male and female founder
123 contribute to the production of eggs equally. The available resources for egg production
124 of a t -year-old colony is R_t . In the first year (0-year-old colony), the parents produce
125 eggs by using the available resources R_0 (J) ($= 2\rho$) (Fig. 2B). The number of first brood
126 eggs F_0 is given by

$$127 \quad F_0 = \frac{\alpha R_0}{r} = \frac{2\alpha\rho}{r}$$

128 where α is the metabolic efficiency of the parents to convert the resources into eggs, r is
129 the cost for producing one egg. For simplicity, we set $\alpha/r = 1$, i.e., $F_0 = 2\rho$. The final
130 family composition of the 0-year-old colony is: a founding male, a founding female and
131 first brood (F_0 eggs).

132 Second year (1-year-old colony): The 1st brood develop into 1-year old larvae, which
133 are too small and undeveloped to contribute to social labor. In the second year, the
134 available resources R_1 (J) are still 2ρ . Parents produce F_0 eggs of the 2nd brood in the
135 second year. Therefore, the final family composition of the 1-year-old colony is: a
136 founding male, a founding female, first brood (F_0 1-year-old larva) and 2nd brood (F_0
137 eggs).

138 In the third year, the 2nd brood are 1-year-old, which do not contribute to social labor.
139 The 1st brood are 2-years-old, at which time they begin to contribute to social labor as
140 helpers.

141

142 **Work performance of helpers.** Work performance P_i (J/year) of a helper offspring
143 increases with age i . Eggs (0-year-old) and 1-year-old larva do not contribute to social
144 labor. Offspring older than 5 years achieve the maximum performance $\beta \cdot \rho$ in their
145 lifetime, where β is the relative work efficiency of helpers compared to the work
146 performance of a parent ρ (Figs. S3 and S4). If β is 1, mature helpers (offspring older
147 than 5 years) have the same work performance as a parent. The 2-4 year old offspring
148 have intermediate performance. Hence, the work performance P_i of a helper at age i
149 (year) is given by

$$150 \quad P_i = \begin{cases} 0 & (i = 0) \\ \frac{\beta\rho(i-1)}{4} & (1 \leq i \leq 5) \\ \beta\rho & (i > 5) \end{cases}$$

151 Total acquired resources R_t (J) are

152 $R_t = 2\rho + \sum H_i \cdot P_i,$

153 where H_i is the number of i -year-old helpers.

154

155 **Reproductive capacity and genomic imprinting.** Relationship between the amount of
156 resources R_t and the number of eggs F_t produced in year t is given by

157
$$F_t = \begin{cases} \frac{\alpha R_t}{r}, & \frac{\alpha R_t}{r} < C_t \\ C_t, & \frac{\alpha R_t}{r} \geq C_t \end{cases},$$

158 where C_t is the reproductive capacity of the parents at colony age t (Fig. 3A).

159 Reproductive capacity of the parents C_t increases with their sexual development.

160 Reproductive capacity of the parents C_t is given by

161 $C_t = K_G \cdot \tanh(t + 1),$

162 where K_G is the maximum fecundity of the parents (Fig. 3A).

163 The maximum reproductive capacity K_G is determined by sexual development of the
164 parents, which is acquired through canalization of the expression of sexual development
165 genes through epigenetic modification (epimark level) E_t (Fig. 3B).

166
$$E_t = \frac{dC_t}{dt} = \frac{4K_G}{\{e^{t+1} + e^{-(t+1)}\}^2}.$$

167 Epigenetic marks are partially inherited by offspring, which leads to a genomic imprinting
168 effect on the sexual development of the offspring. Therefore, imprinting level I_t at colony
169 age t is given by

170 $I_t = \varepsilon E_t.$

171 where ε is the transmission rate of parental epimarks to offspring (Fig. 3B).

172 Antagonistic action of paternal imprinting I_m and maternal imprinting I_f delay the initiation
173 of sexual development of offspring, resulting in prolongation of the offspring's time to
174 become alates τ (Fig. 3C). For simplicity, we assume

175 $I_m = I_f = I_t.$

176

177 **Genomic imprinting and maturation delay of offspring.** The time τ required to become
178 alates, numerically calculated from I_t and its boundary conditions, is given by

179
$$\tau_t = \begin{cases} \tau_{min} & (I_t \leq \tau_{min}) \\ I_t & (\tau_{min} < I_t) \end{cases}.$$

180 The offspring that have spent τ_t after hatching in year t become alates, contributing to the
181 founders' fitness (Fig. 2A). We set $\tau_{min} = 4$ (years) based on the subsocial sister group

182 *Cryptocercus* woodroaches, whose maturity takes about 6 years (Cleveland et al., 1934;
183 Nalepa, 1984). Note that when an offspring stays longer in the colony as a helper, its direct
184 contribution to the yearly fitness is not only delayed, but also its residual life span as a
185 colony founder is shortened. However, its contribution as a helper will increase the
186 production of future offspring (younger brothers and sisters) in the current colony (Fig. 2B).
187 This trade-off between the contribution by staying as helpers and leaving success as
188 alates is key for the evolution of eusociality.

189

190 **Colony fitness and selection process.** Fitness gain $\omega_{G,t}$ of the colony at t is the sum of
191 the reproductive values of dispersing alates with different ages i , such that

$$192 \quad \omega_{G,t} = \sum A_{i,t} \cdot q_{G,i} ,$$

193 where $A_{i,t}$ is the number of alates at age i produced in year t and $q_{G,i}$ is the reproductive
194 value of an alate at age i . In exchange for a prolonged helper period, the reproductive
195 value of an alate $q_{G,i}$ declines with the shortening of its residual life span $(\Phi - i)$ after
196 colony foundation. This discounted reproductive value of an alate at age i is numerically
197 calculated from the fitness function $\omega_{G-1,t}$ of the previous generation $G - 1$, such that

$$198 \quad q_{G,i} = \frac{\sum_{t=0}^{\Phi-i} \omega_{G-1,t}}{\sum_{t=0}^{\Phi-\tau_{min}} \omega_{G-1,t}} .$$

199 In order to calculate the fitness of the first generation $\omega_{1,t}$, we set $q_{1,i} = 1$ because there
200 is no imprinting effects on offspring (all offspring reaching age τ_{min} become alates without
201 delay). Total fitness of generation G is given by

$$202 \quad W_G = \sum_{t=0}^T \omega_{G,t} ,$$

203 where $T = \Phi - \tau$.

204 When the resources exceed the maximum reproductive capacity of the parents K_G ,
205 there is no benefit to the colony since they cannot be used to produce additional eggs.
206 The maximum amount of excess resources ΔR due to the limitation of reproductive
207 capacity K_G is given by

$$208 \quad \Delta R = R_{G,max} - \frac{rK_G}{\alpha} ,$$

209 where $R_{G,max}$ is the maximum yearly resources of a colony at generation G . Mutation from
210 K to $K + 1$ takes place if $\Delta R \geq \frac{r}{\alpha}$ (at least one egg can be produced by the surplus
211 resource) (Fig. 2C, Figs. S5 and S6). Then selection should fix this mutation if $W_G \geq W_{G-1}$
212 (fitness can be increased by mutation). Higher reproductive capacity results from

213 increased epigenetic modification (i.e., stronger canalization (Rice et al., 2016)) of sexual
214 development genes, which results in a higher imprinting level in offspring. Greater
215 imprinting further prolongs the helper period resulting in increased resources in the next
216 generation $G + 1$, which again produces surplus resources ΔR . This whole process may
217 be repeated to increase reproductive capacity K_G as long as the two above-mentioned
218 conditions are satisfied (Figs. S5 and S6). We consider that eusociality arises at the time
219 when the first-brood offspring lose all direct fitness. We also note the time at which the
220 first-brood helpers spend their whole life in the colony, i.e., the appearance of lifelong
221 helpers.

222

223 **Results**

224 We show that genomic imprinting can explain the origin of eusociality, i.e., the first
225 occurrence of a lifelong neuter caste. To consider the evolutionary transition from
226 subsocial to eusocial in the ancestor of termites, we suppose a diploid subsocial
227 organism in which a male and a female cooperatively found a new colony in an enclosed
228 habitat (Figs. 1F, 1G and 2). We developed a genomic imprinting model that predicts the
229 evolution of eusociality via natural selection when parental reproductive capacity is
230 linked to a delay in the sexual development of offspring through transgenerational
231 epigenetic marks that act in a sex-antagonistic manner. We performed evolutionary
232 simulations by running colony generation, where each generation includes a colony life
233 cycle as a part of the simulation (Fig. 2, Fig. S6). Presence of helpers contribute to social
234 labor, which increases the resources available for egg production (Fig. 2B). Selection
235 favors higher reproductive capacity of the parents so as to fully utilize the available
236 resources (Fig. 2C). Acquisition of greater reproductive potential is derived from higher
237 epigenetic modification (canalization) of the genes for sexual development (Fig. 3 A and
238 B). This leads to higher genomic imprinting and thus to the prolonged helper period of
239 the offspring (Fig. 3C).

240 Our numerical algorithm demonstrates that genomic imprinting can drive eusociality via
241 natural selection on colony founders (Fig. 4). The evolutionary transition from subsocial to
242 eusocial systems readily occurs when the epimark transmission rate ε and/or the helpers'
243 work performance β are high (Fig. 4A). Because helpers increase the resources available
244 for egg production (Figs. S3 and S4), natural selection acts on the parents to increase

245 production of alates. Greater reproductive potential requires higher levels of epigenetic
246 modification. Trans-generational carry-over of sex-specific epimarks leads to higher
247 genomic imprinting and thus to a prolonged helper period for offspring. This evolutionary
248 feedback between natural selection and genomic imprinting facilitates the transition from
249 subsociality to eusociality (Fig. 4B). At some generation, the first-brood offspring lose their
250 direct fitness (the origin of eusociality, red arrowheads in Fig. 4 B and C), and then spend
251 their entire life in the colony as helpers (open arrowheads in Fig. 4 B and C). Here the
252 offspring are essentially the extended phenotype of the parents via genomic imprinting.

253 This feedback process generating eusociality creates parent-offspring conflict
254 frequently because the first brood decreases its direct (and even inclusive) fitness by
255 prolonged helper periods (zigzag black and red lines in Fig 4B), but eventually increases
256 its inclusive fitness. Eusociality can still be achieved even if the helpers' work
257 performance is reduced by one-half ($\beta = 0.8 \rightarrow 0.4$), although increase in the rate of
258 parental direct fitness is slowed down (Fig. 4C). When the helpers' work performance is
259 further reduced ($\beta = 0.1$), natural selection does not drive eusociality (Fig. 4D), because
260 helpers cannot produce sufficient resources for increased egg production. Most
261 importantly, the level of genomic imprinting is a key factor driving eusociality; the number
262 of generations required for eusociality (or lifelong helper) to evolve sharply decreases
263 with imprinting strength (i.e., epimark transmission rate ε for a given E_t) (Fig. 4E).
264 Eusociality cannot be achieved if imprinting strength is too low (gray area in Fig. 4E).
265 Also, the development of eusociality is impossible if colony longevity T is too short (Fig.
266 S7), because the contribution of the first brood helpers cannot be used for the production
267 of alates in the colony. It should be noted that when T is larger, it takes more time for
268 eusociality to evolve. This is because it takes more generations for the first brood to
269 become lifelong helpers when they have a longer lifespan ($\Phi = T + \tau_{min}$).

270

271 Discussion

272 The theoretical framework of the present model assumes iteroparity of the founder
273 parents within the nest. This assumption is reasonable because all eusocial insects are
274 iteroparous, which is essential to produce staggered age classes within colonies,
275 enabling older offspring to rear younger siblings. In contrast, the *Cryptocercus*
276 woodroach (the sister group of termites) is semelparous (Nalepa, 1988) and not
277 eusocial. Without iteroparity (no second nor later brood), the evolutionary feedback loop

278 cannot be established. Unlike the Hymenoptera where eusociality evolved multiple
279 times, eusociality evolved only once in the cockroaches (termites) around 150 Myr ago
280 (Bourguignon et al., 2015; Legendre et al., 2015). This single origin of eusociality in
281 Blattodea is likely due to the fact that the acquisition of within-nest iteroparity occurred
282 only once in this taxon, although non-nesting and serial nesting iteroparity are known in
283 some species (Trumbo, 2013).

284 The developmental time to reach maturity should have been long in the subsocial
285 termite ancestor due to a nitrogen-poor wood diet as in wood-feeding cockroaches in
286 which developmental time ranges from three to seven years (Nalepa, 2015). Among
287 wood-feeding cockroaches, the sister-group of termites, *Cryptocercus*, is the only known
288 oviparous cockroach with biparental care and altricial development (Bell et al., 2007;
289 Klass et al., 2008) under biparental care, crucial conditions for the origin of eusociality
290 (Nalepa, 2010). The prolonged altricial period of the offspring creates overlapping
291 broods within a colony providing the opportunity for older brood to help younger sibs
292 (Thorne, 1997). We can reasonably expect that in the termite ancestor the presence of
293 older brood was advantageous for the parents and younger sibs because they provided
294 nest excavation, trophallaxis, allogrooming, defense and other forms of brood care.
295 Therefore, we can expect high work performance β of the helpers in the subsocial
296 ancestral state. In our model, a certain level of work performance β is necessary for the
297 origin of eusociality. Interestingly, however, β can be as low as 0.1 when other
298 conditions are favorable (e.g., $T \geq 15$, $\varepsilon \geq 0.2$, $F_0 \geq 20$, Fig. 4A).

299 As we discussed at the beginning, the evolutionary mechanisms driving the origin of
300 eusociality and selection for the maintenance and later elaboration of eusociality should
301 be discussed separately. We demonstrated that the acquisition of eusociality promotes
302 the production of alates by a colony and also increases the inclusive fitness of the first
303 brood compared with the initial subsocial state (Fig. 4 B and C). In this respect, our
304 findings are consistent with inclusive fitness theory. Most importantly, however, we found
305 that inclusive fitness theory itself cannot explain the origin of eusociality. During the
306 transition from the subsocial to the eusocial state, inclusive fitness of the first brood
307 results in a zigzag line alternating up and down for levels of fitness (Fig. 4 B and C),
308 because there is a time lag between the origin of a prolonged helper period in the first
309 brood offspring and an increase in the reproductive capacity of the parents to utilize the
310 additional resources. This indicates that selection for higher inclusive fitness of the

311 offspring cannot get over the selection valley (it goes down and then up again) and thus
312 cannot generate lifelong helpers.

313 The earlier hypothesis that tried to overcome this selection valley is parental
314 manipulation (Alexander, 1974): parents restrict the reproductive options of some
315 offspring so that they assist in the production of fully fertile offspring. A serious problem
316 with this hypothesis is that counter-selection on the offspring would make them
317 overcome parental manipulation. Moreover, this hypothesis also cannot explain the
318 origin of eusociality, although parental manipulation may increase the parental fitness
319 and the inclusive fitness of the sterile workers in a eusocial state. Selection cannot act
320 on the parents *a priori* in favor of restricting offspring's reproductive development in a
321 subsocial state because it merely reduces the number of fertile offspring and thus their
322 own fitness unless it can be coupled with the subsequent evolution of the ability of the
323 parents to utilize the additional resources for reproduction. A related idea of parental
324 manipulation is the subfertility hypothesis of West-Eberhard (West-Eberhard, 1975),
325 which assumes that subfertile offspring can be produced by inescapable factors such as
326 food shortage and these subfertile offspring would give up reproduction and accept a
327 worker role.

328 Genomic imprinting can be considered one such inescapable factor that produces
329 subfertile offspring. In our genomic imprinting model, natural selection acts on the
330 reproductive capacity of parents so as to increase their direct fitness. Greater
331 reproductive capacity requires higher epigenetic modification of the genes for sexual
332 development (Rice et al., 2016). Sex-specific epigenetic modifications are potential
333 mechanisms underlying sexual dimorphism in various taxa (Hall et al., 2014; Pennell and
334 Morrow, 2013). When sex-specific epimarks that canalize sexually dimorphic
335 development are inherited by the offspring (Rice et al., 2012), sex-antagonistic action
336 (Gadagkar, 2000) of the maternally and paternally inherited epimarks generates the
337 delay of sex expression in the offspring, i.e., the first brood helpers. The offspring's
338 phenotype resulting from the transgenerational epigenetic inheritance is an extended
339 phenotype of the parents, and is thus inescapable for the offspring.

340 Ultimately, whether eusociality spreads in a population depends on the specific
341 benefits of altruistic behavior of the sterile workers relative to their own independent
342 reproduction (Hamilton, 1964). Right at and after the origin of eusociality, the fitness
343 interests of the parents and the offspring coincide with each other (Fig. 4 B and C, Fig.

344 S7): the inclusive (i.e., indirect) fitness of the sterile helpers coincides with the direct
345 fitness of the parents (i.e., colony fitness). From this point on, the subsequent evolution
346 of eusociality is promoted by kin selection, where Hamilton's rule $r > c/b$ is satisfied. In
347 the current numerical analysis, relatedness r is 0.5 because we assume lifelong
348 monogamy of the parents (Boomsma, 2009), and the work performance of helpers β
349 corresponds to the indirect benefit b , while the fitness loss produced by the prolonged
350 helper period τ is the cost c of helpers. Then kin selection (i.e., colony level selection)
351 drives the evolution of extreme morphology and self-sacrificing behavior of soldiers
352 highly specialized in their defensive tasks (Deligne et al., 1981; Šobotník et al., 2012),
353 sophisticated pheromonal communication regulating caste differentiation (Matsumura et
354 al., 1968; Matsuura et al., 2010, 2007; Mitaka et al., 2017), and loss of totipotency, all of
355 which accelerate the reproductive division of labor.

356 This genomic imprinting theory is based on the fact that genomic imprinting operates
357 in caste determination of termites, where sexual development of the offspring is
358 influenced by the sexual phenotypes of parents via transgenerational epigenetic effects
359 (Matsuura, 2020b; Matsuura et al., 2018). Many molecular agents are known to mediate
360 genomic imprinting such as DNA methylation, histone modifications, noncoding RNAs
361 and transcription factors (Ferguson-Smith, 2011; Reik and Walter, 2001). Sex-specific
362 methylation is a potential mechanism underlying sexual dimorphism in various taxa (Hall
363 et al., 2014; Pennell and Morrow, 2013), and a recent molecular study demonstrated that
364 DNA methylation regulates female fecundity in insects (Zhang et al., 2015). In termites,
365 the level of DNA methylation is known to be considerably higher than in any other social
366 insect studied to date (Glastad et al., 2016). Future studies are needed to determine the
367 exact molecular mechanism underlying the genomic imprinting of termites, even though
368 our conclusion holds irrespective of the exact agents.

369 The current theory to explain the origin of eusociality has the potential for broad
370 applications to the origin of sterile workers in various diploid animals such as the
371 ambrosia beetle *Austroplatypus incompertus* (Smith et al., 2018) and the naked mole-rat
372 *Heterocephalus glaber* (Jarvis, 1981). It remains to be investigated in the future whether
373 this theory can be extended to the origin of eusocial Hymenoptera, in which the
374 existence and the role of genomic imprinting in the current caste system are still
375 controversial. This study shows that transgenerational epigenetic inheritance can play a

376 key role in the inception of eusociality and provides a novel framework for studying the
377 evolution of social systems in various organisms.

378

379 **Data Availability.**

380 Major simulation data supporting the findings of this study are available within the paper
381 and Supplementary Information. Simulation data can be generated within the custom-
382 made code and the parameter sets provided. Custom-made simulation code is available
383 via GitHub at (<https://github.com/ItoHiromu/Eusoc-Sim>).

384

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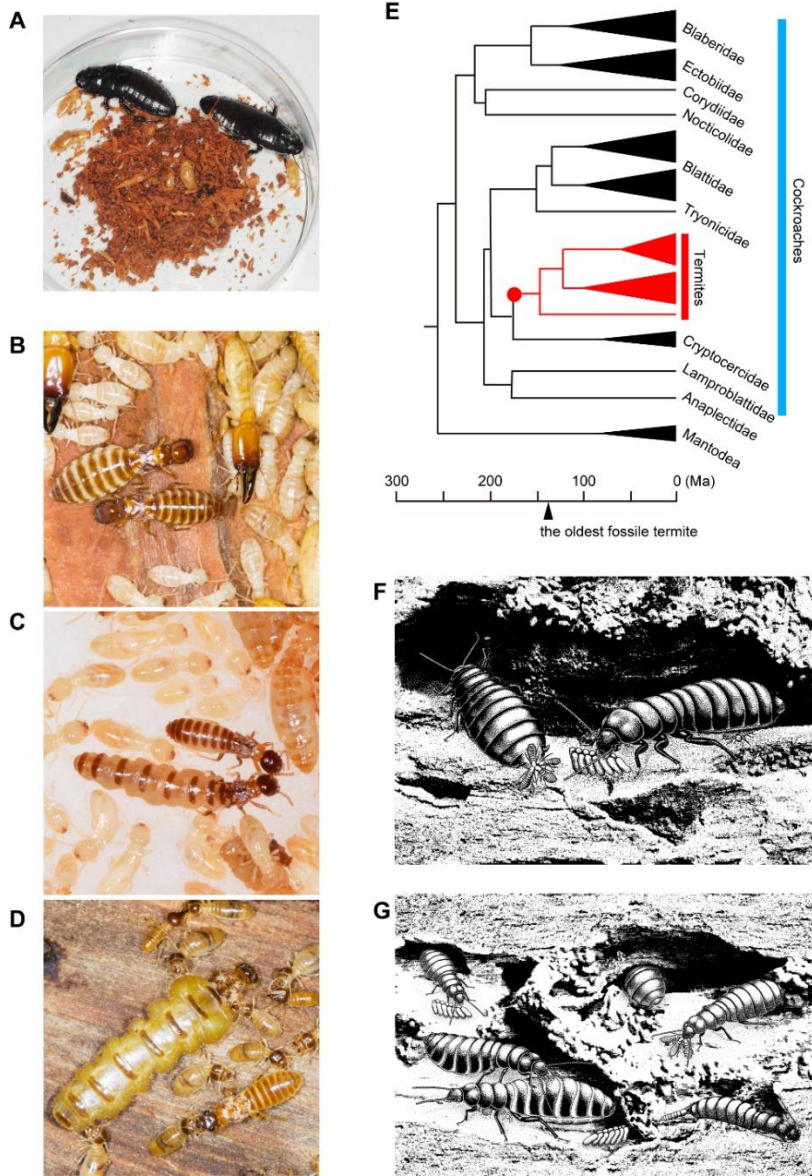
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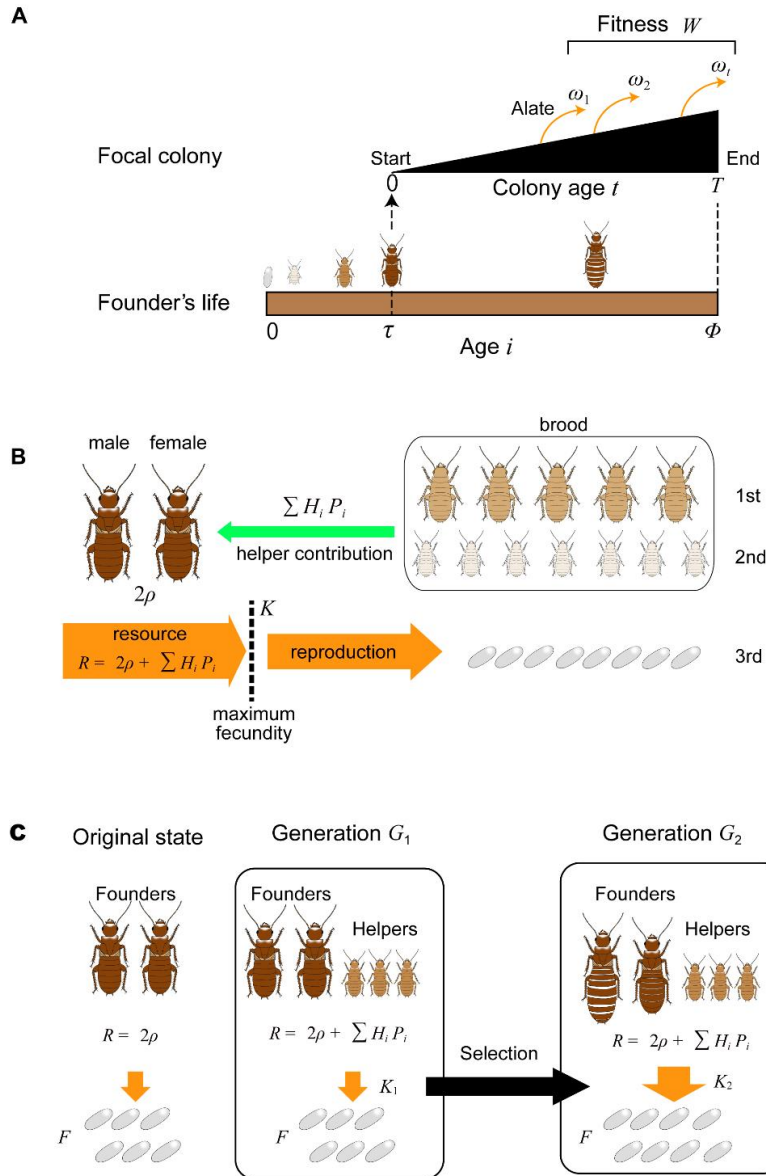
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516

517 **Figures**



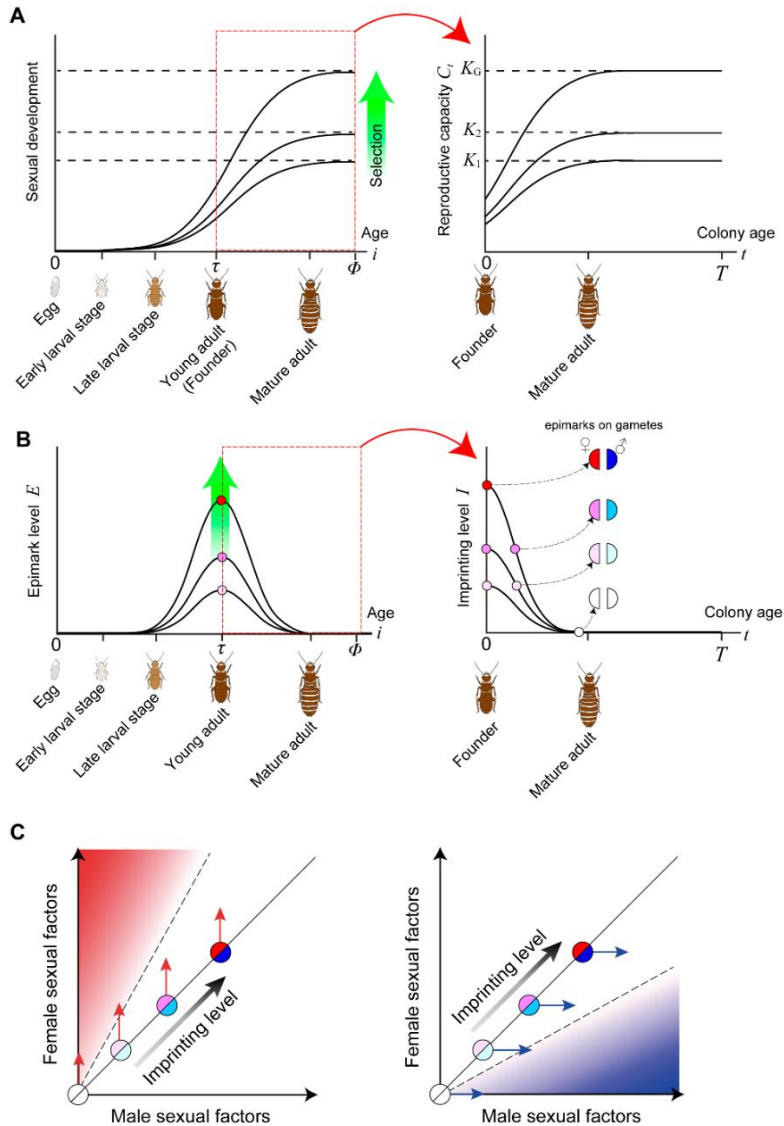
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519 **Figure 1. Termite eusociality originated from a lineage of subsocial woodroach.**
 520 (A) Monogamy in a woodroach *Cryptocercus punctulatus*, which is an oviparous
 521 cockroach with biparental care. (B-D) A primary king (PK) and a primary queen (PQ) of a
 522 damp-wood termite *Zootermopsis nevadensis*, a subterranean termite *Reticulitermes*
 523 *speratus* and a higher termite *Nasutitermes takasagoensis*, respectively. (E)
 524 Phylogenetic placement of termites. Termites are a sister group of Cryptoceridae. (F,
 525 G) Imaginary illustration of the incipient colony (F) and a developed family (G) of the first
 526 termite. The founder female produces a packaged egg mass as in the basal termite
 527 *Mastotermes darwiniensis*. The first brood helpers contribute to the production of
 528 younger sibs through wood excavation, trophallaxis, allogrooming, nest hygiene and so
 529 on. Photos by K.M. Illustrations by H.O and K.M.
 530



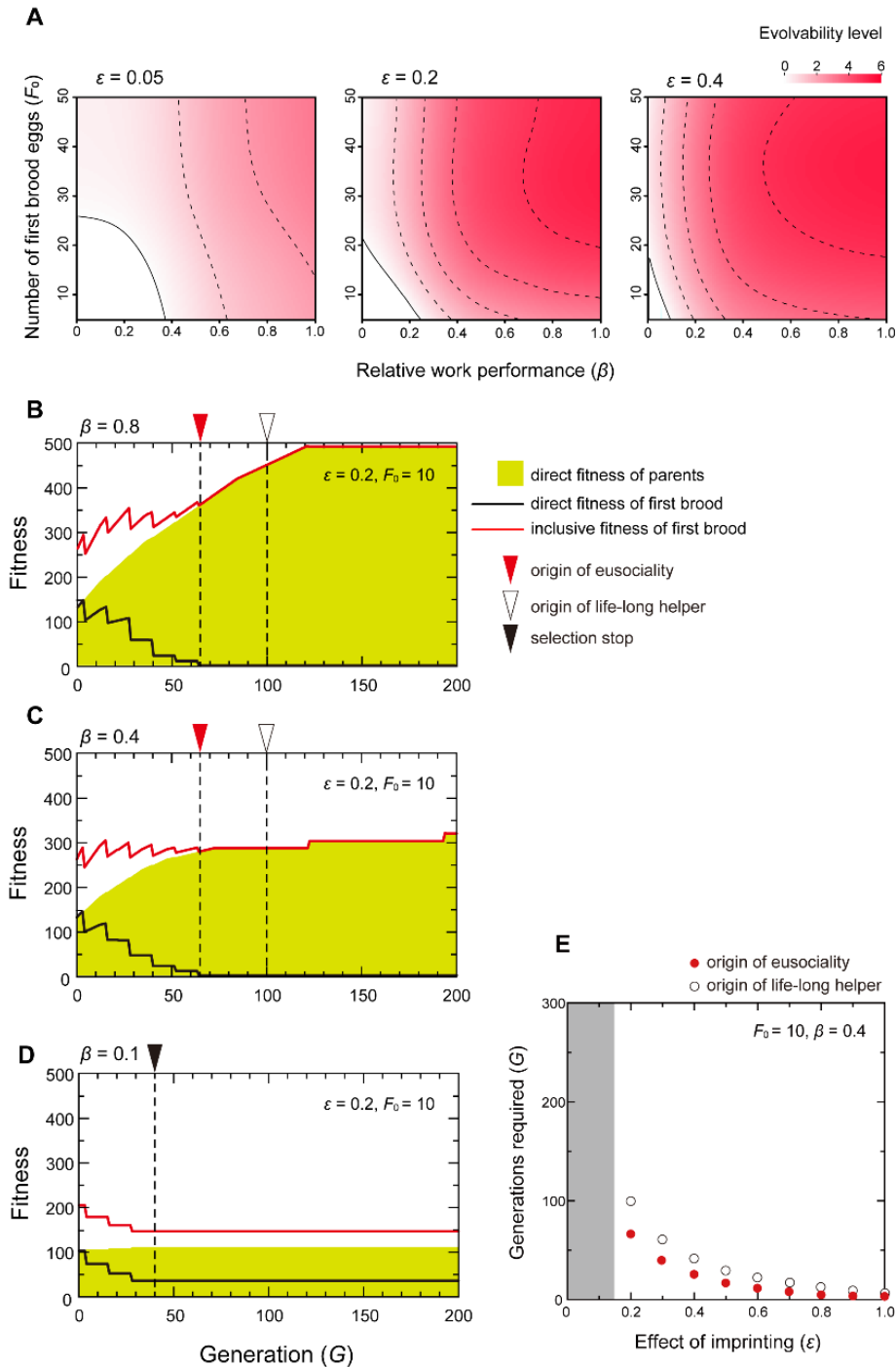
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532 **Figure 2. Schematic view of the model life cycle of a subsocial ancestor of**
 533 **termites just before the origin of eusociality.** (A) Colony life cycle. Individuals
 534 become alates (imagoes) and leave their natal nest at age τ . They disperse and
 535 establish new colonies by pairing with an unrelated individual. The colony produces
 536 alates ω_t at colony age t . Total number of alates produced W during the colony lifespan
 537 $(\Phi - \tau)$ is defined as the fitness of the focal colony. (B) Presence of older brood in the
 538 nest contributes to resource acquisition of parents. (C), Additional resources can be a
 539 selective force for the evolution of higher fecundity of founders. Without helpers, the
 540 founders reproduce by using their own resources 2ρ (left). Even if there were additional
 541 resources from the helpers' contributions, the founders would not be able to use them for
 542 reproduction due to the upper limit of their fecundity K_1 (center). Selection favors higher
 543 fecundity K_2 of the founders so as to fully utilize the additional resources for reproduction
 544 (right). See also Figs. S5 and S6 for the detailed scheme. Illustrations by K.M.
 545



546

547 **Figure 3. The genomic imprinting model for the origin of eusociality.** Sex-
 548 antagonistic action of maternally- and paternally-inherited epimarks retains the offspring
 549 in the neuter state. (A) Sexual development of individuals (left) and reproductive capacity
 550 of founders C_t (right). (B) Development of epimarks in relation to sexual development of
 551 the parents (left) and unerased sex-specific epimarks that carryover to the next
 552 generation through gametes (right). Reproductive capacity of the parents C_t is acquired
 553 through canalization of the expression of sexual development genes through epigenetic
 554 modification E_t . Therefore, E_t is expressed as the derivative of C_t , $E_t = \frac{dC_t}{dt}$. Blue and
 555 red semicircles indicate paternally- and maternally-inherited epimarks, respectively.
 556 Darkness of the color represents the strength of epimarks. (C) Antagonistic action of
 557 maternal and paternal imprinting in the offspring. Illustrations by K.M.



558

559 **Figure 4. Evolvability of eusociality.** (A) The effect of work performance of helpers β
 560 and initial fecundity of the parents F_0 on the evolvability of eusociality. Eusociality is
 561 easily achieved under high epimark transmission rate ϵ and/or high work performance of
 562 helpers β . Evolvability level is evaluated by the level of eusociality acquisition (indicated
 563 by the intensity of red color) when colony longevity T is varied from 10 to 15 years (Level
 564 0: no acquisition; level 6: acquisition under all T cases). Eusociality acquisition is defined
 565 as the appearance of a helper with no direct fitness (inclusive fitness only). (B-D) Fitness

566 dynamics of the parents and the first brood offspring under different work performance
567 levels of helpers β ($T = 13$, $\varepsilon = 0.2$, $F_0 = 10$). Green area indicates the direct fitness of
568 parents (the number of alates produced by a colony). Black and red lines indicate the
569 direct and inclusive fitness of the first brood, respectively. Red arrowheads indicate the
570 origin of eusociality (the appearance of a helper with no direct fitness). Open arrowheads
571 indicate the appearance of a lifelong helper. Black arrowheads indicate the point when
572 selection stops, i.e., the direct fitness of the parents decreases from that of the previous
573 generation in numerical calculation. (E) Effect of genomic imprinting level I_t (i.e., ε for a
574 given E_t) on the generation required to reach eusociality. Red and open circles indicate
575 the origin of eusociality and the appearance of a lifelong helper, respectively. Gray area
576 indicates the region where eusociality is not achieved.
577

578 **Supplementary Information for**

579 **Genomic imprinting drives eusociality**

580

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593 **This PDF file includes:**

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595 Supplementary text

596 1. Transgenerational epigenetic inheritance; a paradigm shift in biology

597 2. Genomic imprinting as a carryover effect of parental epimarks

598 3. Asexual queen succession in termites

599 4. Genomic imprinting in termites

600 5. Additional model explanation: work performance of helpers

601

602 Figures S1 to S7

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609 **Backgrounds**

610 We here introduce the latest studies on the transgenerational epigenetic inheritance and genomic
611 imprinting in termites following the recent review by Matsuura (Matsuura, 2020).

612

613 **1. Transgenerational epigenetic inheritance; a paradigm shift in biology**

614 Evolution by natural selection requires phenotypic variation, inheritance and selection forces.
615 Charles Darwin conceived the theory of natural selection without knowing the agent of
616 inheritance. Biology is traditionally dominated by the idea of genetic determinism, which is
617 focused almost exclusively on genetic inheritance and processes that change gene frequencies.
618 Recent empirical studies have convincingly demonstrated transgenerational epigenetic
619 inheritance in various eukaryotic organisms including yeasts (Grewal and Klar, 1996), plants
620 (Hauser et al., 2011; Miryeganeh and Saze, 2020) nematodes (Remy, 2010; Seroby and
621 Sommer, 2017), mammals (Daxinger and Whitelaw, 2012; Perez and Lehner, 2019) and insects
622 (Mukherjee and Vilcinskas, 2019). The transfer of epigenetic marks from parents to offspring can
623 influence offspring phenotype independent of the DNA sequence (Bonduriansky and Day, 2008).
624 The concept of epigenetic inheritance provides solutions for many previously-unsolved puzzles by
625 circumventing the limitation of genetic inheritance (Bonduriansky and Day, 2008; Jablonka and
626 Raz, 2009; Szyf, 2014). Theoretical studies indicate that epigenetic inheritance is an important
627 factor in evolution that can produce outcomes that are not anticipated under traditional genetics.
628 Therefore, it is apparent that biology is in a major transitional period that will take it forward from
629 the previously narrow perspective.

630 Over the past decade there has been a rapid accumulation of definitive evidence for the
631 molecular mechanisms underlying transgenerational epigenetic inheritance (Greer and Shi, 2012;
632 Liberman et al., 2019; Martin and Zhang, 2007; Miska and Ferguson-smith, 2016; Moazed, 2011).
633 In principle, any molecular change in the zygote other than alterations in DNA sequence could
634 carry non-genetic information including DNA methylation, histone modification, non-coding RNA,
635 prions and microbiota.

636

637 **2. Genomic imprinting as a carryover effect of parental epimarks**

638 The effects of transgenerational epigenetic inheritance on offspring are often sex-specific
639 (Bonduriansky and Day, 2008; Vigé et al., 2008). A phenomenon related to transgenerational
640 epigenetic inheritance is genomic imprinting, whereby epimark transmission depends on parental
641 sex, resulting in parent-of-origin allelic expressions (Gregg et al., 2010; Lawson et al., 2013; Xu et
642 al., 2014). Recent evidence also suggests that imprinting effects can depend on offspring sex
643 (Hager et al., 2008).

644 Kinship theory of genomic imprinting focuses on a conflict (Haig, 2014) between the maternal
645 and paternal genes (see also Holman & Kokko (Holman and Kokko, 2014) and Patten et al.
646 (Patten et al., 2014)). Genomic imprinting can occur as a by-product of another advantageous
647 process such as retrotransposon silencing (Suzuki et al., 2007) or canalization of sexually
648 dimorphic development (Rice et al., 2012) even if imprinting itself has no fitness advantage. The
649 most parsimonious mechanistic explanation for the origin of genomic imprinting would be
650 incomplete erasure of epigenetic modifications, i.e., carryover effects of parental epimarks
651 (Chong and Whitelaw, 2004; Kearns et al., 2000; Rice et al., 2016). Although epigenetic
652 modifications acquired by parents are mostly erased during gametogenesis, which allows
653 reestablishment of epigenetic marks in the next generation, a portion of epigenetic modifications
654 can be inherited through the germline in a wide variety of taxa including mammals (Anway et al.,

655 2005; Morgan and Bale, 2011), insects (Cavalli and Paro, 1998), yeast (Grewal and Klar, 1996)
656 and plants (Miryeganeh and Saze, 2020).

657 The degree of sexual dimorphism will be associated with the degree of sex-specific
658 epigenetic modifications (Deegan and Engel, 2019). Selection favoring a higher degree of sexual
659 dimorphism would lead to a higher imprinting level, if the efficiency of erasure is not changed.
660 This carryover effect of sex-specific parental epimarks on the offspring's development can
661 contribute to the determination of the phenotype (Matsuura et al., 2018; Rice et al., 2013, 2012).

662

663 **3. Asexual queen succession in termites**

664 Transgenerational epigenetic inheritance and genomic imprinting have been attracting more and
665 more attention in the study of insects because many phenomena involving non-genetic
666 inheritance have been found in a number of insect species (Galbraith et al., 2016; Gegner et al.,
667 2019; Matsuura, 2020; Mukherjee and Vilcinskis, 2019). In particular, the effects of parental
668 phenotypes on the caste fate of offspring have been discovered in termites, which provides
669 definitive evidences for non-genetic inheritance (Matsuura et al., 2018). A unique reproductive
670 system named Asexual Queen Succession (AQS) has been identified in several termite species,
671 in which workers, soldiers and alates are produced sexually while neotenic queens arise through
672 thelytokous parthenogenesis and eventually replace the old queens (Hellemans and Roisin,
673 2020; Matsuura, 2017; Matsuura et al., 2009) (Fig. S1). Then, neotenic queens are replaced by
674 subsequent cohorts of asexually-produced neotenic queens. Therefore, as long as the colonies
675 survive, the queens are genetically immortal. This is advantageous for both the queens and other
676 colony members because queens can boost reproduction without inbreeding.

677 After the first report of AQS in the Japanese subterranean termite *R. speratus* (Matsuura et
678 al., 2009), AQS has been continuously found in other *Reticulitermes* species in other continents:
679 *R. virginicus* in the US (Vargo et al., 2012) and *R. lucifugus* in Italy (Luchetti et al., 2013). Time-
680 scaled phylogeny of the genus *Reticulitermes* demonstrated that AQS was absent in the basal
681 lineage but has evolved at least three times independently, in East Asia (ca. 7-5 million years
682 ago), in West Europe (ca. 10-5 million years ago) and in North America (less than 14.1 million
683 years ago) (Dedeine et al., 2016). Recent surveys of the breeding systems of higher termites
684 (Termitidae) in French Guiana have repeatedly identified AQS in Neotropical termitids including
685 *Embiratermes neotenicus* (Syntermitinae) (Fougeyrollas et al., 2015), the humivorous termite
686 *Cavitermes tuberosus* (Termitinae) (Fournier et al., 2016), *Silvestritermes minutus*
687 (Syntermitinae) (Fougeyrollas et al., 2017) and *Palmitermes impostor* (Termitinae) (Hellemans et
688 al., 2019). In all of these seven AQS species, the asexual neotenic queens derive from nymphs,
689 i.e., the sexual pathway.

690 Why has AQS evolved repeatedly in phylogenetically distant lineages? The origin of AQS
691 requires the simultaneous evolution of two distinct traits: parthenogenetic capacity and the
692 developmental priority for parthenogenetic daughters to develop into secondary queens. Then a
693 question emerges as to why parthenogenetic daughters and sexually-produced daughters differ
694 in their developmental propensity. Nozaki et al. (2018) asked if in a non-AQS species, *R.*
695 *okinawanus*, the female offspring produced by tycho-parthenogenesis (i.e., occasional
696 parthenogenesis) differentiate into secondary queens (Nozaki et al., 2018). Interestingly a
697 significantly higher proportion of parthenogenetic daughters developed into neotenic queens
698 (nymphoid queens) than sexually produced females (Nozaki et al., 2018). This suggest that the
699 developmental propensity of parthenogenetic daughters to become neotenic queens existed prior
700 to the origin of AQS, which could explain why AQS evolved repeatedly in phylogenetically distant
701 lineages.

702

703 **4. Genomic imprinting in termites**

704 Influence of parental phenotypes on the caste fate of offspring is known in the genus
705 *Reticulitermes* (Hayashi et al., 2007; Kitade et al., 2010). For instance, the daughters produced
706 by queens' parthenogenesis and the daughters produced by the mating of nymph-derived queens
707 and worker-derived males develop exclusively into nymphs. On the other hand, most of the
708 daughters produced by the mating of worker-derived queens and nymph-derived males develop
709 into workers. The theory of genomic imprinting explains the effects of parental phenotypes on
710 caste fate of the offspring (Matsuura et al., 2018). Its prediction matches exactly with empirical
711 data from both lab and field studies.

712 As shown in the scheme (Fig. S2), the theory of genomic imprinting consists of two stages: 1)
713 development of phenotype-specific parental epimarks and 2) influence of parental imprinting on
714 the development of offspring. Nymph-derived reproductives obtain higher levels of epimarks so
715 as to canalize expression of sexual characters than ergatoids (worker-derived reproductives) (Fig.
716 S2A). Then the maternally- and paternally-inherited epimarks influence the relative expression of
717 growth regulatory genes (ϵ_g : growth factors) to sex regulatory genes (ϵ_s : sexual factors), and thus
718 determine the caste fate of offspring (Fig. S2B). Growth with sexual development directs
719 individuals to the sexual pathway (nymphs), while growth without sexual development restricts
720 individuals to the neuter caste (workers). The double maternal imprinting of parthenogenetic
721 daughters leads them to the sexual pathway in AQS species.

722 The predictions of genomic imprinting model match well both with the caste differentiation
723 patterns of the AQS species *R. speratus* (Hayashi et al., 2007) (Fig. S2B) and those of the non-
724 AQS species *R. kanmonensis*, *R. yaeyamanus* and *R. okinawanus* (Kitade et al., 2010). Genomic
725 imprinting clearly explains why the daughters carrying only maternal chromosomes have the
726 developmental propensity to become neotenic queens rather than daughters carrying both
727 paternal and maternal chromosomes.

728 Genomic imprinting explains why parthenogens carrying only maternal chromosomes pre-
729 adaptively have the epigenetic and thus developmental advantage to become neotenic queens
730 (Matsuura et al., 2018; Nozaki et al., 2018). Many factors are known to mediate genomic
731 imprinting such as DNA methylation, histone modifications, noncoding RNAs and transcription
732 factors (Ferguson-Smith, 2011; Reik and Walter, 2001). The DNA methylation levels in termites
733 are considerably higher than other hemimetabolous insects (Harrison et al., 2018). Moreover,
734 termites shows caste- and sex-specific DNA methylation patterns (Glastad et al., 2016). The DNA
735 methyltransferases DNMT1 and DNMT3 are known to be involved in maintenance of and
736 mediating *de novo* DNA methylation, respectively (Goll and Bestor, 2005; Yan et al., 2015). RNA-
737 seq analysis of *R. speratus* revealed sex- and caste-dependent expression patterns of the DNA
738 methyltransferases, where alates have higher expression of *Dnmt1* than workers in females but
739 not in males. Alates also showed significantly higher expression of *Dnmt3* than workers in males
740 but not in female (Mitaka et al., 2020). These results seem to support the theory of genomic
741 imprinting.

742

743 **5. Additional model explanation**

744 **Work performance of helpers.** Within-nest iteroparity creates the overlapping broods within a
745 colony, which provides the opportunity for older brood to contribute to the production and growth of
746 younger sibs (Thorne, 1997). The presence of older brood is advantageous for the parents and
747 younger sibs rather than imposing a deleterious effect because they provide nest excavation,
748 trophallaxis, allogrooming, defense and other forms of brood care. Therefore, we can reasonably
749 expect a high work performance β of the helpers in the subsocial ancestral state.

750 Work performance P_i (J/year) of a helper offspring increases with age i . Eggs (0-year-old) and
751 1-year-old larvae cannot contribute to social labor. Offspring older than 5-years achieve their

752 maximum possible performance $\beta \cdot \rho$, where β is the relative work efficiency of helpers compared
753 to the work performance of a parent ρ . If β is 1, mature helpers have the same work performance
754 as a parent. 2-4 year old offspring have intermediate performance. Thus the helper performance
755 P_i of a helper at age i (year) is given by (Fig. S3)

756

$$757 \quad P_i = \begin{cases} 0 & (i = 0) \\ \frac{\beta \rho^{(i-1)}}{4} & (1 \leq i \leq 5) \\ \beta \rho & (i > 5) \end{cases} \quad (\text{S1})$$

758

759

760 We also investigated the effect of the curvatures s of age-dependent increase in work
761 performance P_i on the origin of eusociality (Fig. S4),

762

$$763 \quad P_i = \begin{cases} 0 & (i = 0, 1) \\ \frac{\beta \cdot \rho}{4} (1 - s) & (i = 2) \\ \frac{\beta \cdot \rho}{2} & (i = 3) \\ \frac{\beta \cdot \rho}{4} (3 + s) & (i = 4) \\ \beta \cdot \rho & (5 \leq i) \end{cases} \quad (\text{S2})$$

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765 There is no qualitative change in the outcome when the curvatures s varies from 0 to 1 (the
766 results were omitted).

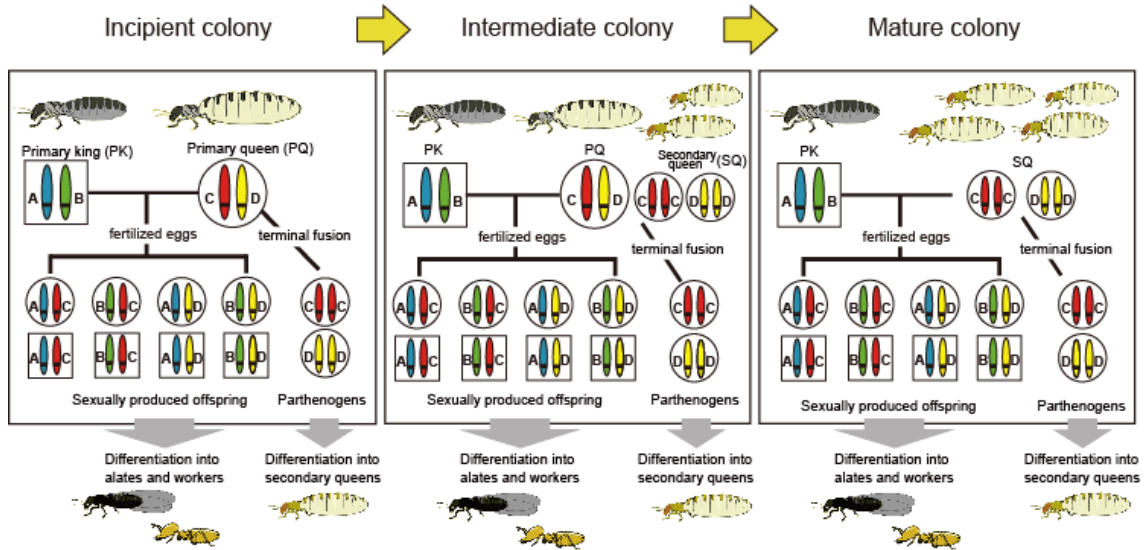
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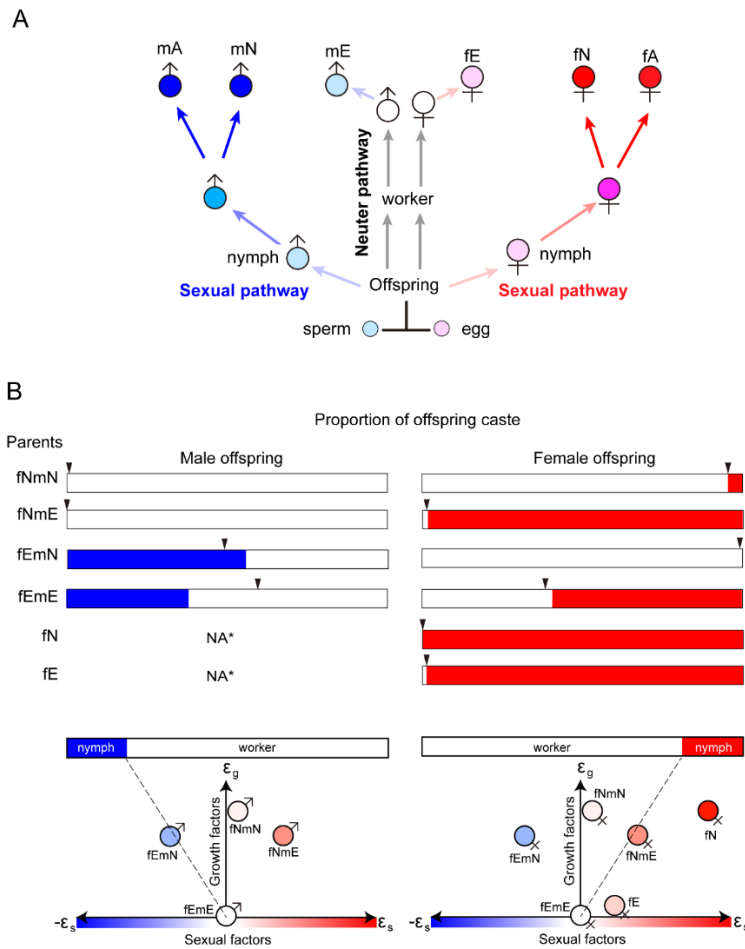
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774 **Fig. S1. Asexual queen succession in termites.** Secondary queens produced asexually by the
775 primary queen differentiate within the colony and supplement egg production, eventually,
776 replacing the primary queen (Matsuura, 2017; Matsuura et al., 2009). This breeding system
777 enables the primary queen to maintain her full genetic contribution to the next generation, while
778 avoiding any loss in genetic diversity from inbreeding.

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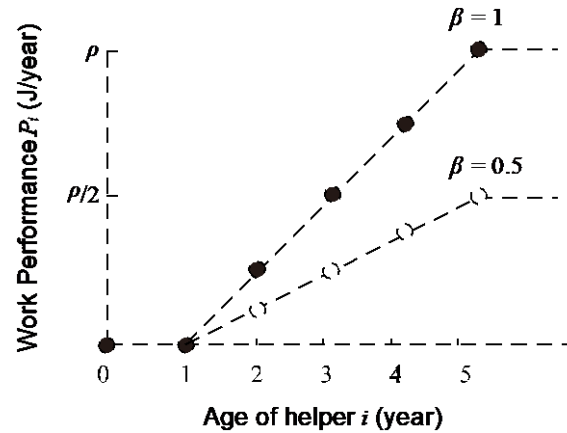
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783 **Fig. S2. Genomic imprinting and caste determination in termites.** (A) Caste differentiation
 784 and establishment of sex-specific epimarks. Alates (male: mA; female: fA) and nymphoids (male:
 785 mN; female: fN) develop with the full canalization of sexual development, while ergatoids (male:
 786 mE; female: fE) develop by a single sexual molt. Blue and red arrows indicate the development of
 787 male- and female-specific epimarks, respectively, and darkness of the color represents the
 788 strength of epimarks. (B) Combination of parental phenotypes and outcome of offspring caste
 789 (e.g., fEmN: female ergatoid and male nymphoid). The caste differentiation patterns predicted by
 790 the genomic imprinting model (bar graphs) and the empirical results (arrowheads) of *R. speratus*
 791 (Hayashi et al., 2007). *Parthenogenesis produces only female offspring. Expression levels of
 792 growth regulatory genes (ϵ_g) and sexual regulatory genes (ϵ_s) of the male- and female-offspring.
 793 Modified from Matsuura et al. (Matsuura et al., 2018).

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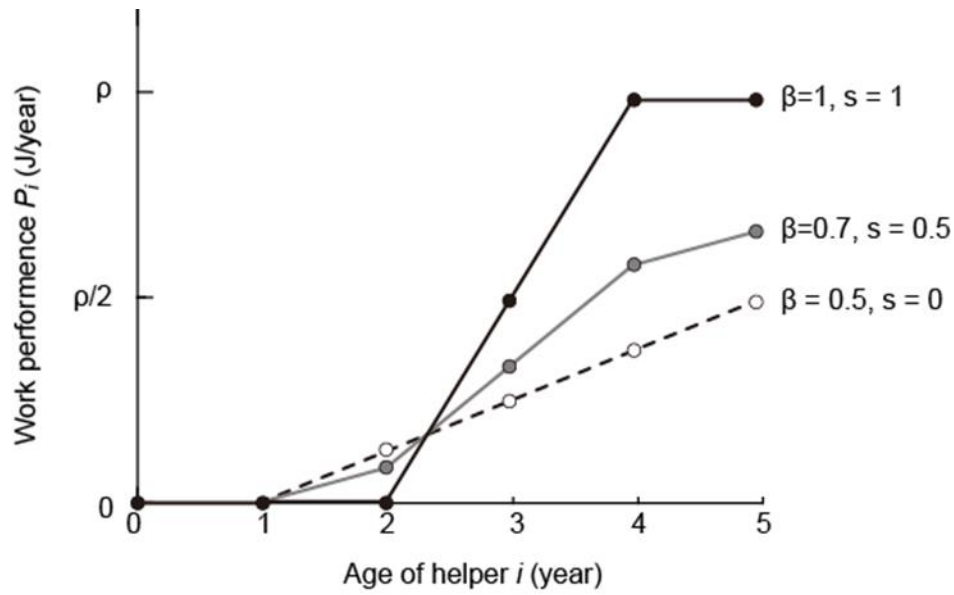


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799 **Fig. S3. Relationship between age and work performance of helpers.** Work performance P_i
800 (J/year) of a helper increases with age i (year), where 0-year-old and 1-year-old helpers do not
801 contribute to social labor. Offspring older than 5 years achieve their maximum possible
802 performance $\beta \cdot \rho$, where β is the relative work efficiency of helpers to the work performance of a
803 parent ρ . If β is 1, mature helpers (offspring older than 5 years) have the same work performance
804 as a parent (closed circles). The 2-4 year old offspring have intermediate performance levels.
805 Hence, the work performance P_i of a helper at age i (year) is given by Equation (S1).

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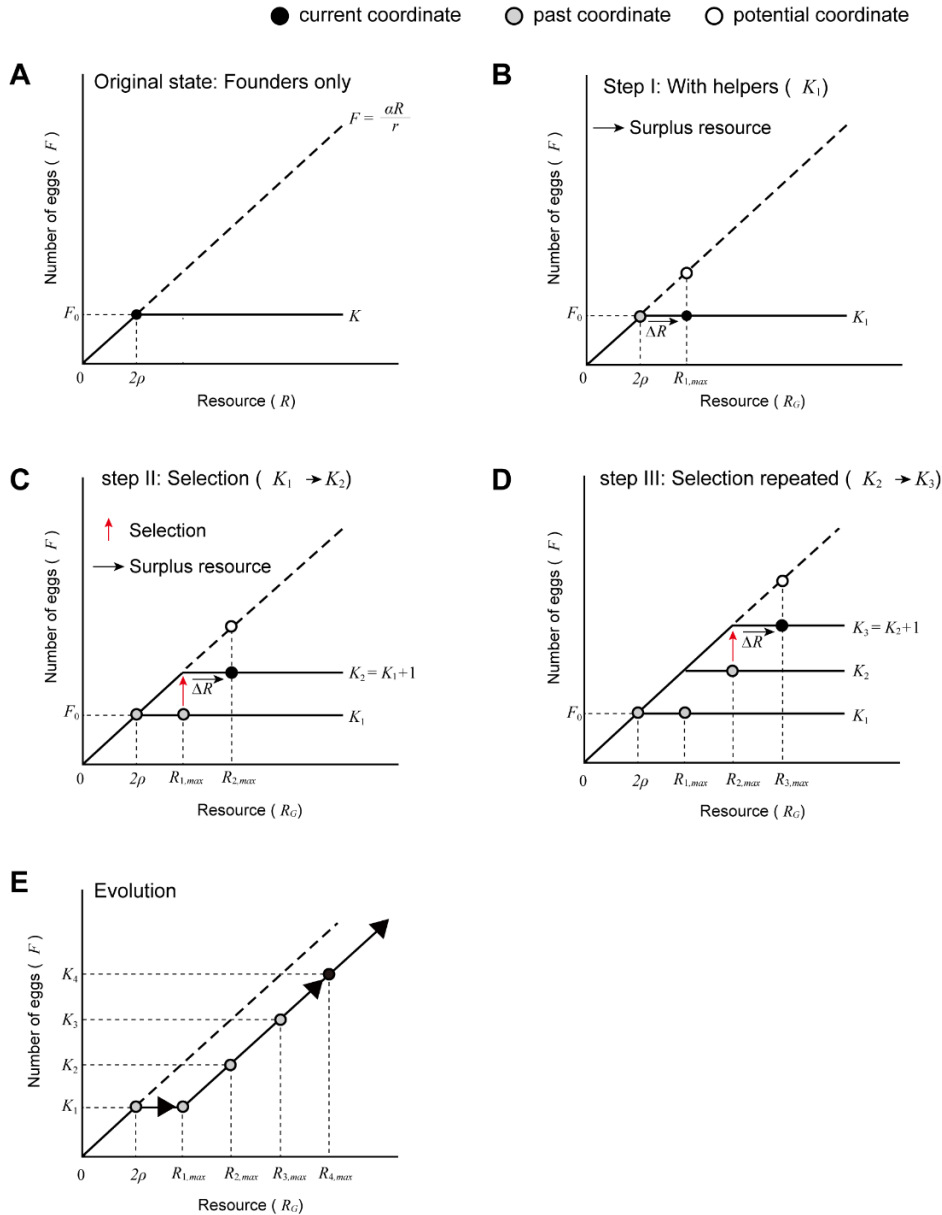
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809 **Fig. S4. Relationship between age and work performance of helpers.** The work performance
810 P_i of a helper at age i (year) is given by Equation (S2).

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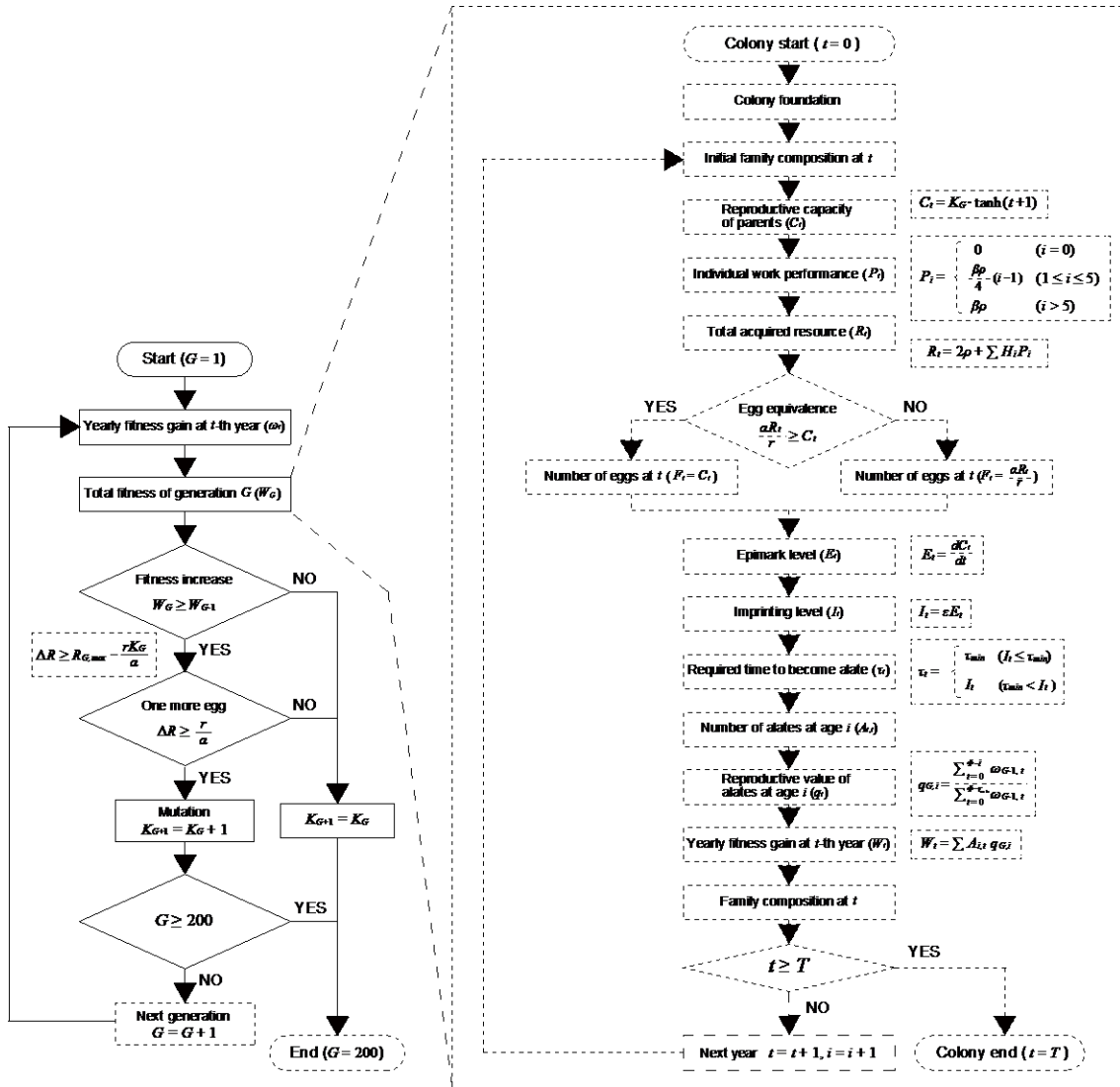
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815 **Fig. S5. Selection scheme.** (A) Original state. Without helpers, the founders reproduce by using
 816 their own resources 2ρ . A monogamous pair of a male and a female produce F_0 eggs using their
 817 own resources 2ρ . (B) Step I (generation G_1). Presence of helpers contribute to social labor, which
 818 increases the resources available ΔR for egg production. Nevertheless, the parents can produce
 819 only F_0 eggs because of limitations on maximum reproductive capacity K_1 . (C) Step II (generation
 820 G_2). Selection favors higher reproductive capacity of the parents so as to fully utilize the available
 821 resources ($K_1 \rightarrow K_2$). Acquisition of greater reproductive potential is derived from higher epigenetic
 822 modification (canalization) of the genes for sexual development^{30,31}. This leads to higher genomic
 823 imprinting and thus to the prolonged helper period of the offspring. Therefore, selection for higher
 824 K moves the coordinate from $(R_{1,max}, K_1)$ to $(R_{2,max}, K_2)$. (D) Step III (generation G_3). In the same
 825 way as step II, selection favoring higher K to utilize the surplus resources moves the coordinate
 826 from $(R_{2,max}, K_2)$ to $(R_{3,max}, K_3)$. (E) The evolutionary process. Trace of the evolution of
 827 reproductive capacity starting from $K_1 (= F_0)$.

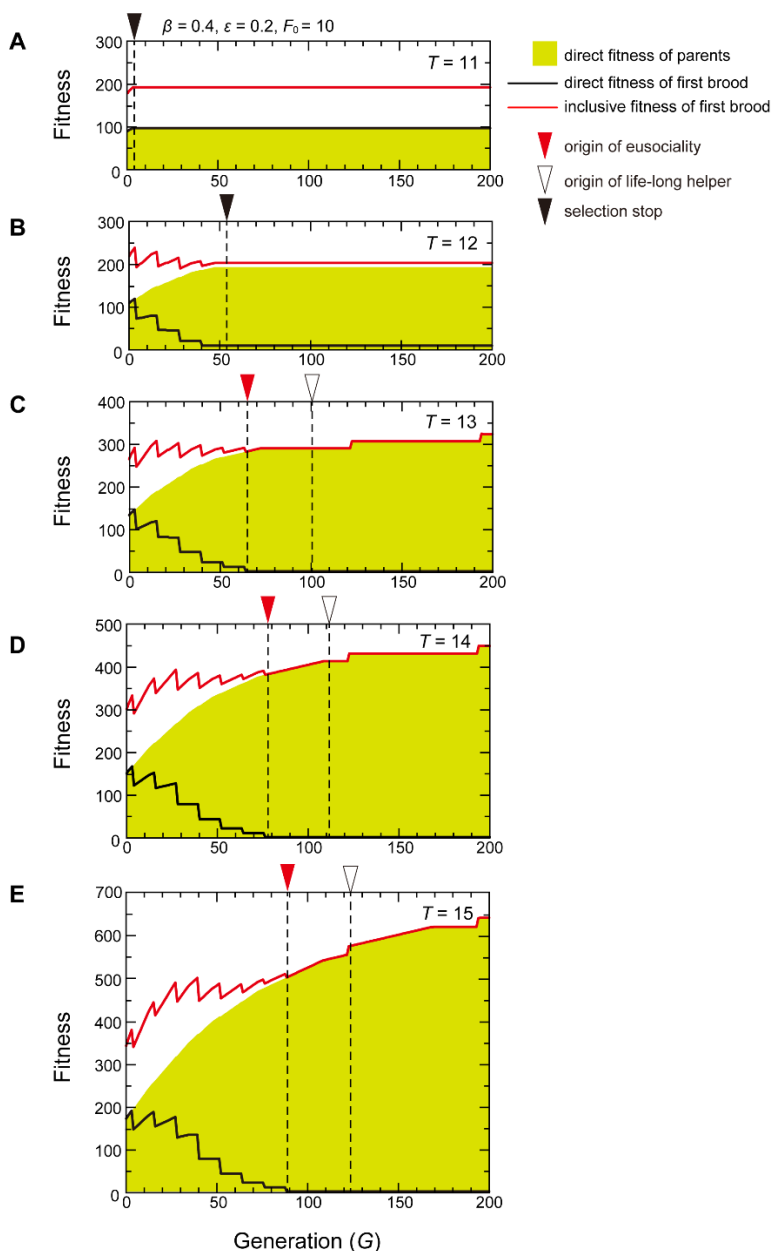


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830 **Fig. S6. Simulation flow.** See Model for the detailed procedure.

831



832

833 **Fig. S7. Colony longevity and evolvability of eusociality.** Fitness dynamics of the parents and
 834 the first brood offspring under different values of colony longevity T . ($\beta = 0.4, \varepsilon = 0.2, F_0 = 10$). (A,
 835 B) Colony lifespan is too short for the inception of eusociality. Selection stops, that is, the direct
 836 fitness of the parents decreases, at generation $G = 5$ when $T = 11$ (A) and at $G = 53$ when $T = 12$
 837 (B) without reaching the threshold for eusociality. (C-E) Colony lifespan is sufficient for the evolution
 838 of eusociality. Eusociality originates at $G = 65$ when $T = 13$ (C), at $G = 77$ when $T = 14$ (D) and at
 839 $G = 89$ when $T = 15$ (E). Green area indicates the direct fitness of parents (the number of alates
 840 produced by a colony). Black and red lines indicate the direct and inclusive fitness of the first brood,
 841 respectively. Red arrowheads indicate the origin of eusociality (the appearance of a helper with no
 842 direct fitness). Open arrowheads indicate the appearance of lifelong helper. Black arrowheads
 843 indicate the point when selection stops, i.e., the direct fitness of the parents is lower than that of
 844 the previous generation in numerical calculation.

845 **Table S1. The parameters of the genomic imprinting model**

Symbol	Definition
i	Age of offspring (years)
Φ	Longevity of individuals (years)
τ	Time from birth to dispersal (years)
t	Colony age (year), i.e., time after colony foundation
T	Longevity of a colony, i.e., $\Phi - \tau$ (years)
ω_t	Fitness gain of the colony at t
W	Total fitness of a colony
ρ	Work performance of an adult (a founding male or a founding female)
R_t	The available resources for egg production of a t -year-old colony
α	Metabolic efficiency of the parents to convert the resources into eggs
r	Cost of producing one egg
F_t	The number of eggs produced in year t
P_i	Work performance (J/year), i.e., the total resources (J) acquired by a single helper at age i in one year
β	Relative work performance of a helper to that of a parent ρ
H_i	Number of i -year-old helpers
C_t	Reproductive capacity (eggs/year) of the parents of a t -year-old colony, that is, the maximum number of eggs produced in year t
K_G	The maximum reproductive capacity, i.e., reproductive capacity of fully-matured parents of generation G
E_t	Epimark level of the parents of a t -year-old colony, that is, the time derivative of C_t (Fig. 3B)
ε	Relative strength of epigenetic inheritance
I_t	Imprinting level of the offspring produced in year t
$A_{i,t}$	The number of i -year-old alates produced in year t
$q_{G,i}$	The reproductive value of the i -year-old alate

847

848 **Table S2. Parameter combinations in figures**

Figure	Simulation results	Varied Parameters	Fixed Parameters
Fig. 4A	Evolvability of eusociality	$\beta, F_0, T, \varepsilon$	
Fig. 4B-D	Fitness dynamics	β	F_0, ε, T
Fig. 4E	Generations required for the origin of eusociality	ε	β, F_0, T
Fig. S7	Fitness dynamics	T	β, F_0, ε

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A



B



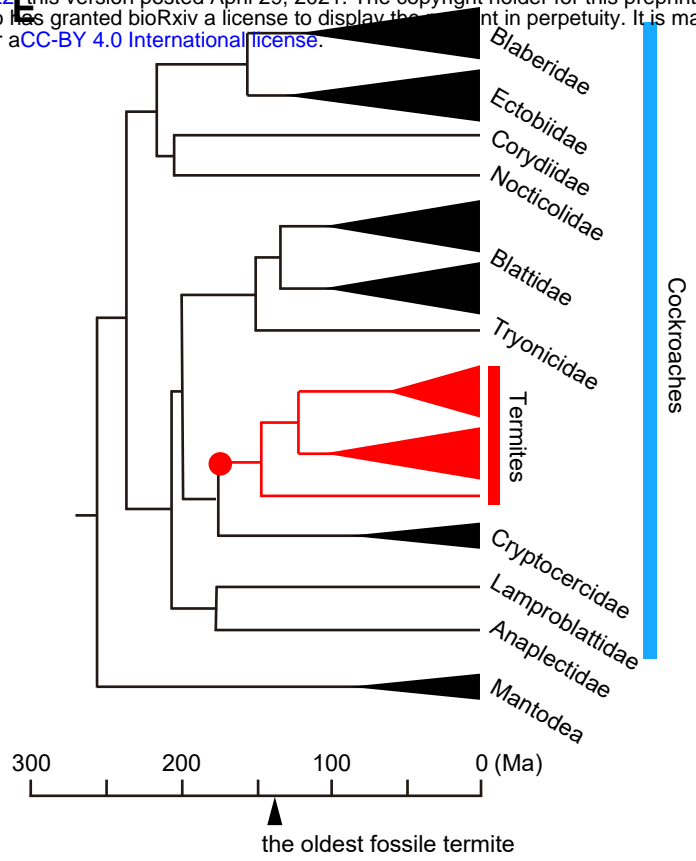
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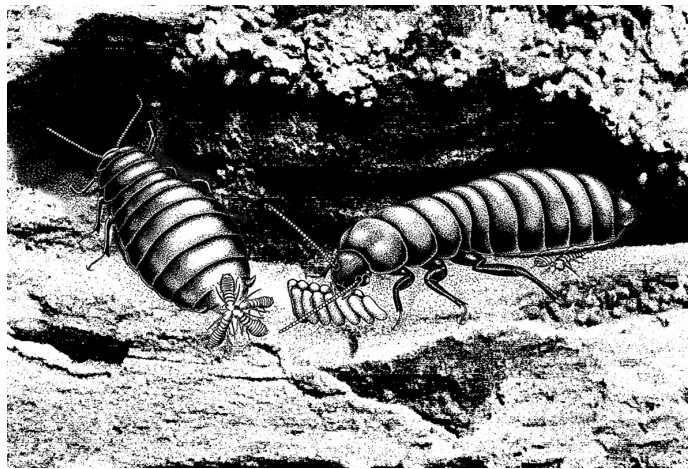
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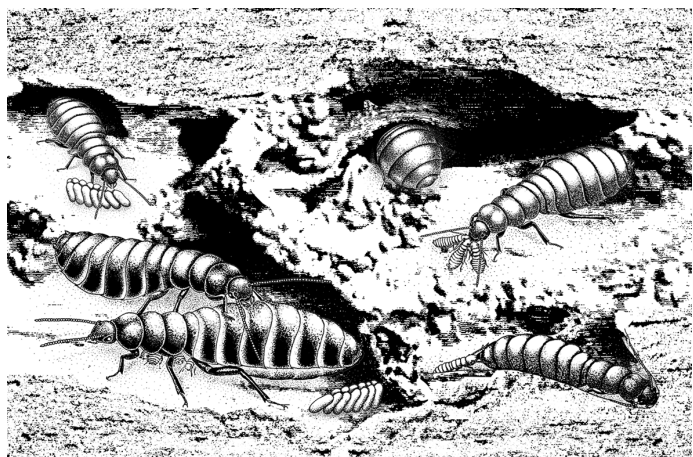


Fig. 1

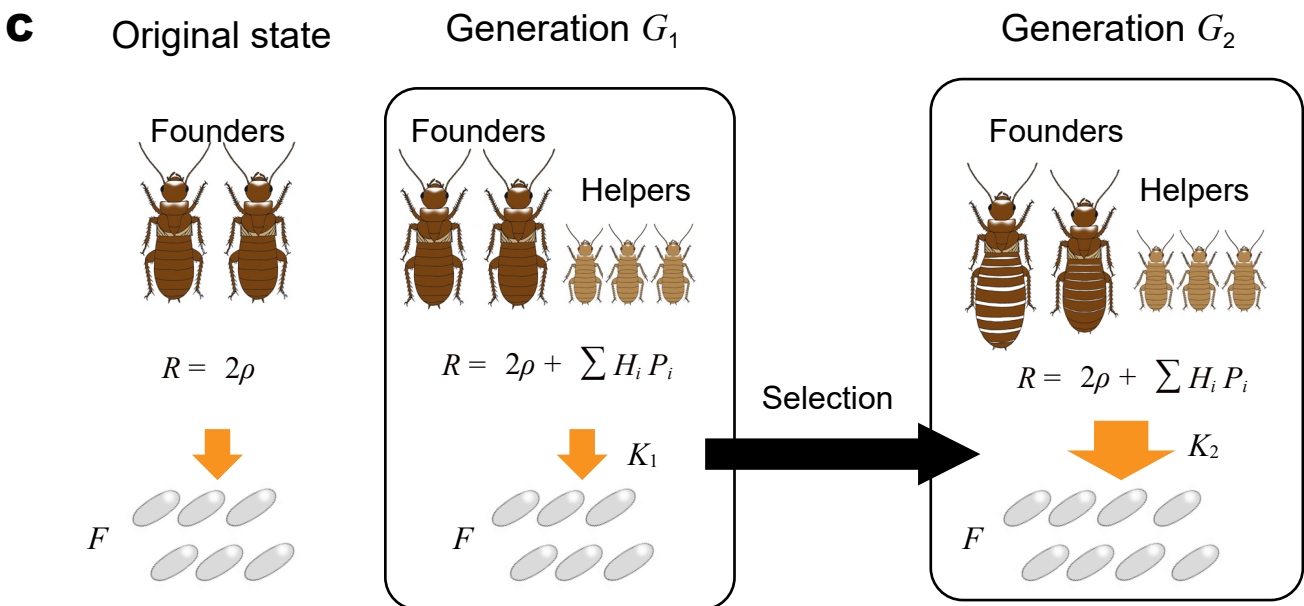
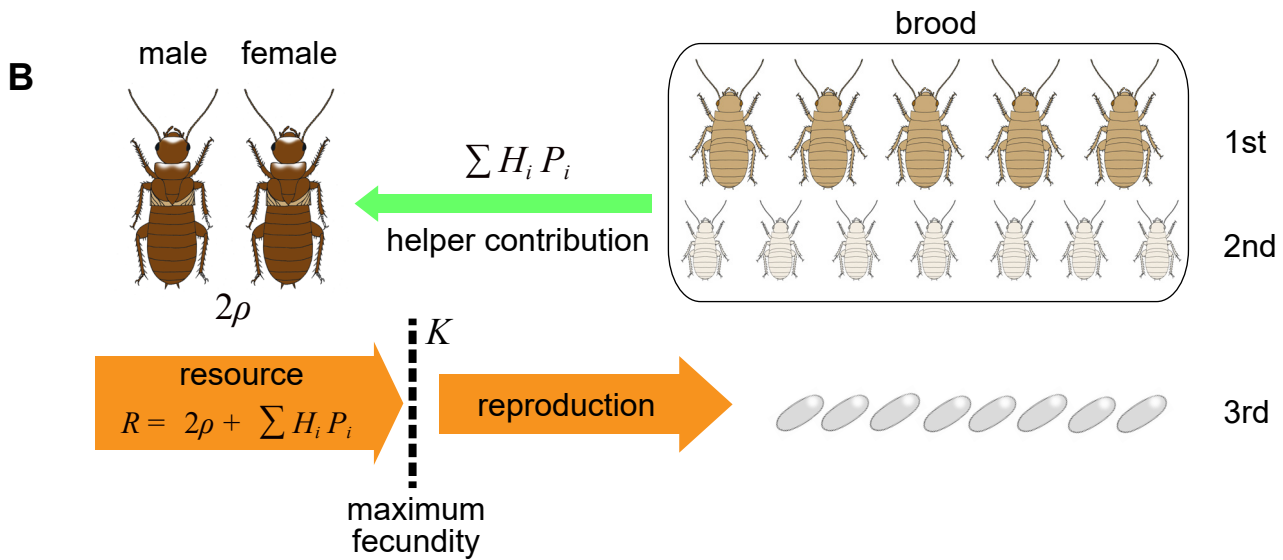
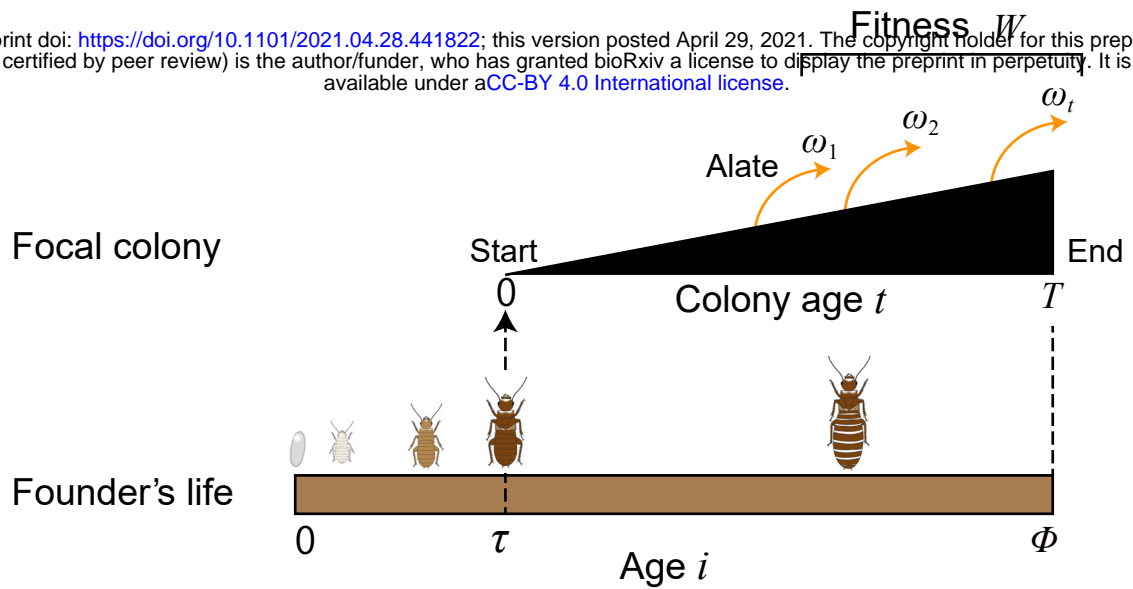


Fig. 2

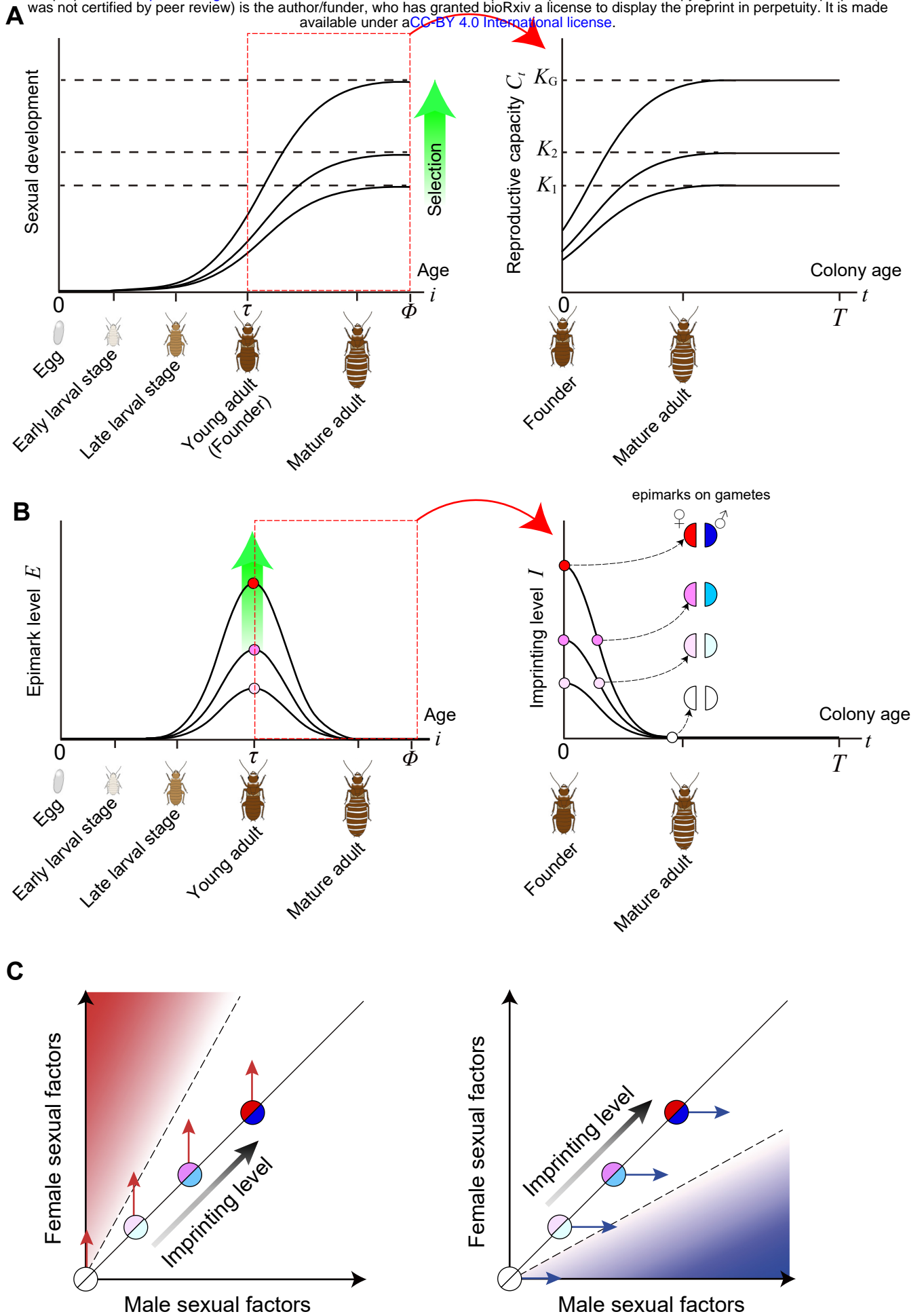


Fig. 3

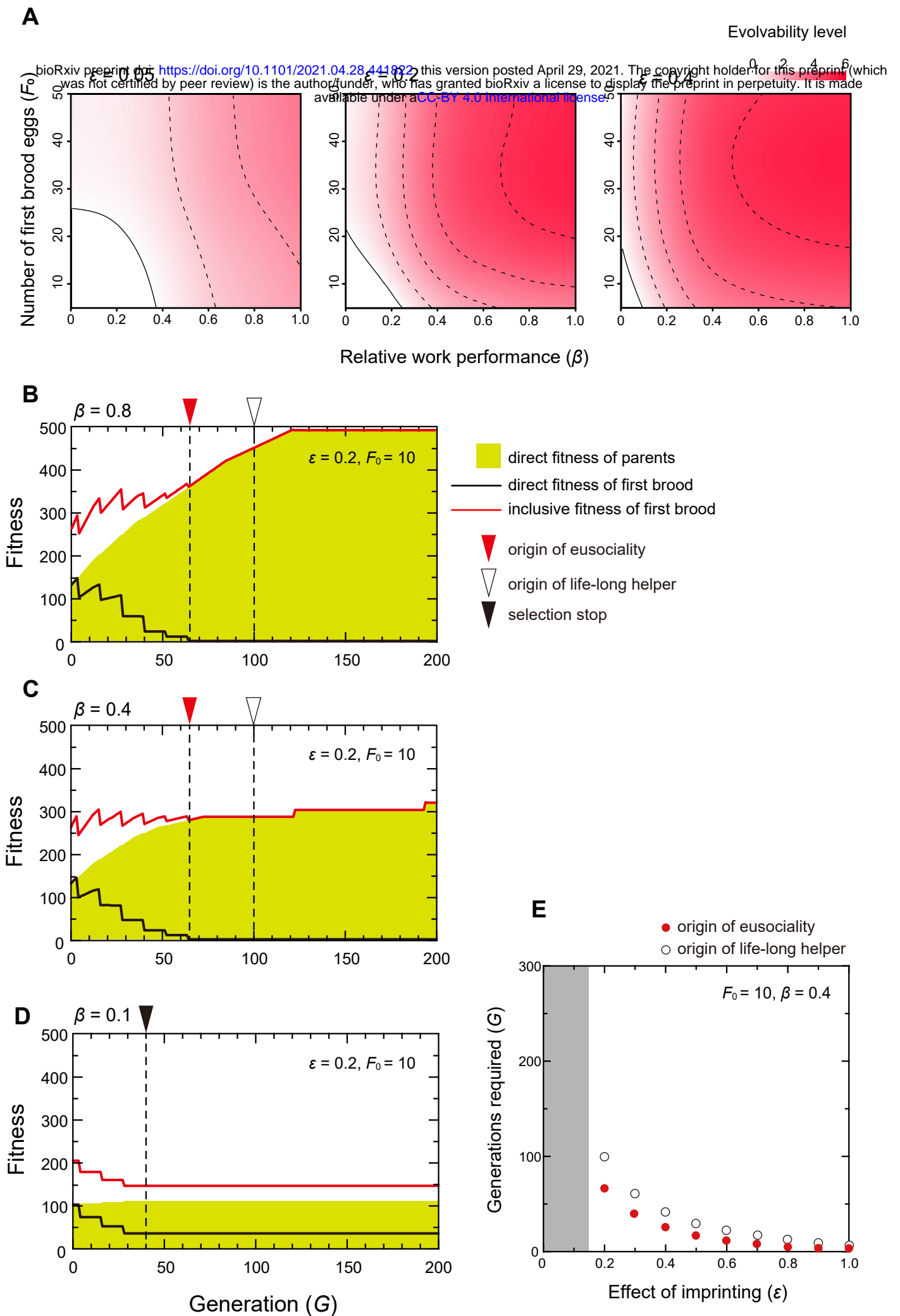


Fig. 4