1   **Title: Factors promoting maternal trophic egg provisioning in**

2   **non-eusocial animals**

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15   The number of text pages: 27

16   The number of figures: 6

17   The number of tables: 1

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Abstract

The adaptive function of trophic egg-laying is generally regarded as extended parental investment to the offspring. However, the evolutionary factors promoting trophic egg-laying are still unclear, because the amount of maternal investment per offspring should be ideally equal between smaller offspring with trophic eggs and larger offspring without any additional investment. Several authors have suggested that trophic egg-laying should evolve only when egg size is constrained, but this hypothesis has not been evaluated. We investigated the evolutionary mechanisms of trophic egg-laying by two different approaches. First, we evaluated morphological constraints on egg size in two sibling ladybird species, *Harmonia axyridis*, which is known to produce trophic eggs, and *H. yedoensis*. Second, we theoretically predicted the optimal proportion of trophic eggs to total eggs and egg size in relation to environmental heterogeneity, predictability of environmental quality, and investment efficiency of trophic egg consumption. The intra- and interspecific morphological comparisons suggest that morphological constraints on the evolutionary determination of egg size are weak at best in the two ladybird species. Moreover, we theoretically showed that small egg size and trophic egg-laying are favoured in heterogeneous environments when mothers cannot adjust egg

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37 size plastically. We also showed that even a small reduction in investment efficiency

38 makes a trophic egg strategy unlikely, despite relatively high environmental predictability.

39 We conclude that trophic egg provisioning may be a flexible maternal adaptation to a

40 highly heterogeneous environment rather than a response to a morphological constraint

41 on egg size.

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Introduction

Trophic eggs (also called nurse eggs) are non-developing eggs or egg-like structures

produced for offspring consumption (Crespi 1992). Strictly speaking, trophic egg-laying

is an evolved maternal phenotype, not simply the unavoidable production of

non-developing eggs that happen to be eaten by offspring (Crespi 1992, Perry and

Roitberg 2006). Trophic egg-laying occurs in diverse animal taxa with various parental

care systems (e.g., non-social and eusocial arthropods, gastropods, amphibians, fishes;

reviewed by Perry and Roitberg 2006), although it is often confined to only a few species

within a taxonomic group (Elgar and Crespi 1992). In general, the adaptive function of

trophic egg-laying is regarded as extended parental investment to the offspring

(Alexander 1974, Polis 1984). However, the amount of maternal investment per offspring

should be ideally equal between smaller offspring with trophic eggs and larger offspring

without any additional parental investment (Baur 1990, Dixon 2000). Therefore,

evolutionary factors promoting trophic egg-laying, instead of larger offspring size, are

still not understood.

Several studies have suggested that trophic egg-laying should evolve only when egg

size is constrained (Alexander 1974, Polis 1984, Mock and Parker 1997, Dixon 2000).

64   Morphological constraints on egg size such as the size of the ovipositor or pelvic aperture

65   may prevent small females from producing large eggs (Congdon and Gibbons 1987) and

66   thus may lead to the evolution of trophic egg-laying. Moreover, other hypotheses based

67   on the density effect of competing offspring (Parker and Begon 1986) and the

68   physiological constraints (Sakai and Harada 2001) also explain why larger mothers

69   produce larger offspring. In fact, many field studies of diverse animal taxa have

70   documented positive correlations between maternal size and offspring size (Fox and

71   Czesak 2000). However, no studies have evaluated whether mothers that produce trophic

72   eggs exhibit such constraints on maternal body size.

73   Adaptive mechanisms that might promote trophic egg-laying should be considered

74   in situations where morphological constraints on egg size are not critical. Trophic

75   egg-laying occurs in several groups of eusocial Hymenoptera (Sakagami 1982,

76   Hölldobler and Wilson 1990, Crespi 1992), but it is difficult to examine the adaptive

77   significance of trophic eggs in eusocial systems because complicated conflicts among

78   colony members may obscure the origin and evolution of trophic eggs (Crespi 1992). By

79   contrast, in non-eusocial taxa, the adaptive function of trophic eggs for offspring survival

80   has been examined by focusing on environmental heterogeneity (Kudo and Nakahira

81   2005, Perry and Roitberg 2005a). In fact, studies have documented that females of some

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82   non-eusocial species that face highly heterogeneous environments adopt a trophic egg

83   strategy (e.g., Crump 1981; Kudo and Nakahira 2004). However, maternal fitness

84   between the two strategies, (1) producing small offspring with trophic eggs and (2)

85   producing large offspring without any additional investment, has not been compared

86   explicitly. For such a comparison, a model that can predict which strategy is

87   evolutionarily stable in a heterogeneous environment needs to be developed.

88   Such a model must take into account the unavoidable costs and limitations that are

89   likely to accompany a trophic egg strategy in a heterogeneous environment. As in any

90   strategy involving adaptive phenotypic plasticity (Berrigan and Scheiner 2004, Marshall

91   and Uller 2007), cues that reliably predict future environment conditions must be present

92   for flexible trophic egg provisioning to evolve. However, the environment that the

93   offspring will face is not always predictable, especially in species in which offspring and

94   adult individuals occupy different niches (Werner and Gilliam 1984, Fischer et al. 2011).

95   Although to reduce the level of uncertainty, mothers can collect information that will be

96   useful in making provisioning decisions (Dall et al. 2005), in a variable environment, a

97   certain level of uncertainty is likely to persist. Moreover, even when mothers can collect

98   information accurately, it may be difficult to compensate for environmental quality in

99   through provisioning without specialized morphology and physiology for trophic egg

100   production, such as distinct ovariole structure and cellular development. Indeed, in the

101   predatory ladybird *Harmonia axyridis* which lacks specialized trophic egg structure

102   (Osawa and Yoshinaga 2009), mothers can manipulate the proportion of trophic eggs

103   depending on the prey availability, but the ratio of trophic to viable eggs is variable even

104   in the highly standardized laboratory conditions (Perry and Roitberg 2005a). As a result,

105   the possibility exists that mothers will provision the 'wrong' amount of resources to their

106   offspring. Furthermore, consumption of trophic eggs is likely to involve some waste of

107   maternal resources (Elgar and Crespi 1992). However, no study incorporating such costs

108   and limitations has thus far examined the conditions that favour the trophic egg-laying.

109   In this study, we investigated the evolutionary mechanisms that favour trophic

110   egg-laying by making morphological comparisons and by mathematical modelling. First,

111   we compared egg size and maternal body size both intra- and interspecifically in two

112   sibling ladybird species, *Harmonia axyridis* Pallas and *Harmonia yedoensis* Takizawa.

113   Adult body size is quite similar in these two ladybird species (Sasaji 1998), and the

114   hatched larvae of both species eat clusters of sibling eggs, both undeveloped eggs and

115   developing eggs with delayed hatching (Kawai 1978, Osawa 1992a, Osawa and Ohashi

116   2008). The sibling egg consumption by hatchlings can be regarded as an adaptive

117   maternal phenotype in both *H. axyridis* (Perry and Roitberg 2005a) and *H. yedoensis*

118   (Noriyuki et al. 2011). If morphological constraints on egg size exist, a positive

119   correlation between egg size and maternal body size would be expected within each

120   species, because smaller mothers cannot produce larger eggs (Fox and Chezak 2000,

121   Fischer et al. 2002, Noriyuki et al. 2010). In addition, if morphological constraints

122   prevent *H. axyridis* females from producing large eggs, then the similar-sized *H.*

123   *yedoensis* females should not be able to produce eggs larger than those of *H. axyridis*.

124   Furthermore, in females of both species we also examined the ovariole number, which is

125   an important determinant of egg size for a given maternal body size in insects (Gilbert

126   1990, Stewart et al. 1991a). Thus, we evaluated the role of morphological constraints by

127   comparing and assessing morphological traits in these two sibling ladybird species.

128   Second, we constructed a mathematical model to predict the optimal proportion of

129   trophic eggs and egg size that mothers should produce. Under spatially and temporally

130   heterogeneous environments for offspring survival, we investigated how reliable the

131   environmental cues available to the mother have to be for a trophic egg strategy to be

132   favoured by selection. Additionally, we incorporated the fact that a certain proportion of

133   maternal resources provided as trophic eggs are not consumed by the offspring and

134   examined whether natural selection favours trophic egg-laying despite its cost. Finally, on

135   the basis of the results of these different two approaches and the findings of previous

136   studies, we propose a reasonable explanation for the widespread occurrence of trophic

137   egg-laying in non-eusocial animals.

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139   **Methods**

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141   Morphological measurements

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143   The generalist predator *H. axyridis* and the specialist predator *H. yedoensis* are sibling

144   species with sympatric distributions in central Japan (Noriyuki et al. 2011). Females of

145   the two species produce undeveloped eggs which are consumed by the sibling hatchlings

146   (Osawa and Ohashi 2008). However, the precise developmental mechanisms regulating

147   the production of undeveloped eggs are not fully understood. Indeed, it is possible that

148   gamete incompatibility and sperm limitation cause the failure of fertilization (e.g., Wedell

149   et al. 2002). Moreover, eggs can be infected by male-killing bacteria and killed male

150   embryos appear as infertile eggs in both *H. axyridis* (Majerus et al. 1998) and *H.*

151   *yedoensis* (N. Osawa, unpublished data), although uninfected females also produce

152   certain proportion of undeveloped eggs. The absence of micropyles is one criterion used

153   to categorize an egg as trophic in the Hymenotera and Heteroptera (e.g., Gobin et al. 1998,

154   Kudo et al. 2006), but in *H. axyridis*, micropyles are present in the shells of both

155   developing and undeveloped eggs (Osawa and Yoshinaga 2009). In addition, there is no

156   special feature of the spatial distribution of undeveloped eggs within the clutch in *H.*

157   *axyridis* (Perry and Roitberg 2005a). However, the proportion of undeveloped eggs

158   increases when *H. axyridis* mothers face the low resource availability (Perry and Roitberg

159   2005a) and consumption of undeveloped eggs enhance the survival of hatchlings

160   especially when aphid density is low (Osawa 1992a), in a manner consistent with a

161   definition of adaptive trophic egg provisioning (Perry and Roitberg 2006). Although *H.*

162   *yedoensis* mothers have not been definitely proved to produce trophic eggs in the strict

163   sense (cf. Perry and Roitberg 2006), the consumption of undeveloped eggs greatly

164   enhances prey capture performance in *H. yedoensis* hatchlings, suggesting that the

165   production of undeveloped eggs has evolved as an adaptive maternal phenotype

166   (Noriyuki et al. 2011). Therefore, even though precise proximate mechanisms have not

167   been identified, the production of undeveloped eggs in *H. axyridis* and *H. yedoensis* can

168   be regarded as an adaptive maternal strategy for the offspring survival.

169   We collected 10 *H. axyridis* adults at the Botanical Garden of Kyoto University,

170   Kyoto (135°47'E, 35°02'N), and 25 egg clusters of *H. yedoensis* at Hieidaira, Shiga

171   (135°83'E, 35°02'N), in May 2008. We obtained eggs from the adults and the egg

172   clusters, and reared the resulting offspring at each stage in plastic cups (13 cm wide, 10

173   cm high) to the adult stage at 25 ºC, 16L:8D, and about 70% relative humidity. We

174   provided the larvae with a surplus of frozen *Ephestia kuehniella* Zeller eggs (Beneficial

175   Insectary, Inc., Redding, California, USA). We randomly chose 54 newly-emerged and

176   unmated individuals (27 females and 27 males) of *H. axyridis* and 48 newly-emerged and

177   unmated individuals (24 females and 24 males) of *H. yedoensis* from the stock for the

178   experiment. We used first-generation offspring because (1) there were not enough adults

179   of *H. yedoensis* in the original field collection for a valid statistical analysis, and (2) it

180   allowed us to use larval morphology to confirm the identities of the two species, which

181   are almost impossible to distinguish on the basis of adult morphology (Sasaji 1998).

182   To obtain eggs from the first-generation adults, we reared mated females

183   individually with a surplus of frozen eggs at 25 ºC, 16L:8D, and about 70% relative

184   humidity. We used 10 eggs from each of five different clutches laid by each female for

185   data analysis, except if the number of eggs in a clutch was less than 10, then all eggs in

186   that clutch were measured. In the case of a female that laid fewer than five clutches, we

187   measured 10 eggs from each clutch that she laid. We measured both egg height (h) and

188   width (r) under a stereo microscope (Carl Zeiss® SV-11 APO) to the nearest 0.025 mm.

189   We estimated egg size as the egg volume calculated using the formula $hr^2\pi/6$ (mm^3;

190   Takakura 2004). We measured body length with a slide calipers to the nearest 0.01 mm

191   and used as maternal body size. After a female died or had laid five clutches, we

192   examined her number of ovarioles under the stereo microscope.

193

194   Statistical analysis

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196   We took into account the fact that the sizes of eggs from the same clutch or laid by the

197   same mothers are not statistically independent. To test for a correlation between maternal

198   body size and egg size, we adopted a regression model with more than one value of the

199   dependent variable (egg size) per value of the independent variable (maternal body size;

200   Sokal & Rohlf 1995). We used nested analysis of variance (nested ANOVA) with mothers

201   within ladybird species, and with clutches within mothers, to compare egg size between

202   ladybird species. We analyzed the effects of maternal body size and ladybird species on

203   ovariole number by analysis of covariance (ANCOVA). All statistical analyses were

204   carried out with JMP® 7 (SAS Institute Japan).

205

206   The model

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208   We present the simplest theoretical framework for the evolution of trophic egg-laying that

209   incorporates environmental heterogeneity, environmental predictability, and investment

210   efficiency of trophic eggs. We assume that mothers cannot adjust egg size plastically.

211   This assumption is applicable to many kinds of animals because ovariole or pelvic

212   aperture size should remain unchanged in a given individual female. In fact, egg size

213   appears to be inflexible within individual females in many animals, such as land snails

214   (Baur 1988, Baur and Raboud 1988), insects (Stewart et al. 1991a, 1991b, Dixon and Guo

215   1993, Soares et al. 2001), and birds (Christians 2002), and this inflexibility may be tied to

216   ovariole or pelvic aperture size. Even though some species are able to manipulate egg size

217   in response to the quality of the oviposition site (Leather and Burnand 1987, Fox et al.

218   1997, Mizumoto and Nakasuji 2007), plastic adjustment of egg size is uncommon in

219   animal taxa and the degree of the egg size variation seems to be highly constrained (e.g.,

220   Kawecki 1995). In addition to morphological factors, physiological mechanisms of

221   oogenesis may also constrain the immediate adjustment of egg size. Therefore, we

222   assume instead that egg size can evolve to an optimal value and that mothers can produce

223   trophic eggs to deal with an adverse environment. We assume that trophic eggs and viable

224   eggs are the same size, because no general size difference trend has been reported.

225   Moreover, we assume that trophic and viable eggs provide equal food quality for

226   offspring survival, although possible differences in chemical composition and function

227   between these eggs have not been examined. For simplicity, we assume that the total

228   amount of maternal resources that can be allocated to the offspring as viable eggs and

229   trophic eggs is the same for all females and fixed to 1.

230   To model the simplest possible variable environment, we examine an environment

231   with only two states: good and poor. The relationship between investment per offspring

232   and offspring fitness differs between the two environments because of biotic or abiotic

233   factors. Moreover, we do not distinguish between spatial and temporal variation. We

234   specify that the minimum viable offspring size is smaller in the good environment than in

235   the poor environment, because an offspring should require fewer resources to become

236   established in the more favourable environment (Fox et al. 1997). We also assume that,

237   for offspring of a given size, offspring fitness is greater in the good environment than in

238   the poor environment (McGinley et al. 1987). Furthermore, we assume that low levels of

239   maternal investment result in zero fitness for offspring because they need a threshold

240   amount of resource to survive, and that fitness approaches an asymptote at high levels of

241   parental investment because offspring cannot make full use of excess resources (Smith

242   and Fretwell 1974, Parker et al. 2002). Thus, we describe the relationship between

243   offspring fitness S and viable egg size in the good environment by $S_G(e) = 1 - (1/e)^2$ and

244   in the poor environment by $S_{\mathrm{P}}(e) = 1 - (k/e)^2$, where the subscripts G and P indicate the

245   good and the poor environment, respectively, e is viable egg size and trophic egg size, and

246   k is a constant that specifies the difference in quality between the two environments. To

247   make the labels 'good' and 'poor' biologically feasible, we assume $k > 1$ such that

248   offspring survive better in a good environment. We assume that individual females

249   experience the two habitat types, good and poor, in the proportion p and $1 - p$,

250   respectively.

251   We define environmental predictability, q, as the probability that maternal

252   assessment of the environmental quality is correct. Specifically, we assume that when

253   mothers incorrectly assess a poor environment as a good environment, then they do not

254   provision trophic eggs although the offspring may need them to survive. Conversely,

255   when maternal assessment of the good environment is wrong, then mothers may

256   provision unneeded trophic eggs, causing per offspring maternal investment to exceed the

257   optimal value (Table 1). For simplicity, we assume that predictability q is constant across

258   environmental situations. If $q = 1$, then mothers can assess the environmental quality

259   perfectly and provision the optimal proportion of trophic eggs in each environment; in

260   contrast, if $q = 0.5$, then mothers provision trophic eggs with a probability of 0.5

261   irrespective of the environmental quality. Because $q < 0.5$ is not realistic, we consider

262   only situations with $0.5 \leq q \leq 1$ in the analysis.

263   From the above assumptions it follows that the ratio of trophic eggs to the total

264   amount of maternal investment is given by $p(1-q)t + (1-p)qt = t(p+q-2pq)$, where t

265   is the ratio of trophic eggs to the amount of maternal investment when maternal

266   assessment is wrong in the good environment or correct in the poor environment (that is,

267   the amount of resource when mothers 'evaluate' the environment as poor; Table 1).

268   Similarly, the number of viable eggs in an environment that mothers evaluate as poor is

269   given by $\{p(1-q)(1-t) + (1-p)q(1-t)\}/e = \{(1-t)(p+q-2pq)\}/e$. Hence, per

270   offspring maternal investment in an environment that mothers evaluate as poor is given

271   by $e + t(p+q-2pq)\delta \div \{(1-t)(p+q-2pq)\}/e = \{1 + \delta t/(1-t)\}e$, where δ is the

272   investment efficiency of trophic egg consumption, defined as the proportion of the

273   trophic egg amount consumed by the offspring. Because the total amount of maternal

274   investment is fixed to 1, the amount of maternal investment that is provided as viable eggs

275   in both environments is given by $1 - t(p+q-2pq)$. Therefore, maternal fitness can be

276   described as the product of offspring number times the probability of offspring survival in

277   each environment:

278    $W(e,t) = \dfrac{1 - t(p+q-2pq)}{e}\left\{ p\left(qS_{\mathrm{G}}[e] + (1-q)S_{\mathrm{G}}\left[\left(1 + \dfrac{\delta t}{1-t}\right)e\right]\right) + (1-p)\left(qS_{\mathrm{P}}\left[\left(1 + \dfrac{\delta t}{1-t}\right)e\right] + (1-q)S_{\mathrm{P}}[e]\right)\right\}$

279 **Results**

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281   Morphological comparisons

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283   Mean female body length was not significantly different between *H. axyridis* (mean ± SE

284   = 7.03 ± 0.09 mm, *n* = 27) and *H. yedoensis* (7.24 ± 0.10 mm, *n* = 24; Student's *t* test, t_{49}

285   = −1.67, *P* = 0.10). Female body length and egg volume were not significantly related in

286   either species (linear regression analysis, *H. axyridis*: $F_{1,25}$ = 0.16, *P* = 0.69, r^2 = 0.003; *H.*

287   *yedoensis*: $F_{1,22}$ = 0.25, *P* = 0.62, r^2 = 0.005; Fig. 1). Mean egg volume was significantly

288   smaller in *H. axyridis* (mean ± SE = 0.2478 ± 0.0011 mm^3, *n* = 1150) than in *H. yedoensis*

289   (0.3481 ± 0.0013 mm^3, *n* = 1046; nested ANOVA, $F_{1,49}$ = 5458.62, *P* < 0.0001; female

290   code [species]: *df* = 49, *F* = 53.9136, *P* < 0.0001; clutch code [female code]: *df* = 187, *F* =

291   6.3250, *P* < 0.0001). There were significant maternal body size and species effects on

292   ovariole number but no maternal body size × species interaction was detected (ANCOVA,

293   maternal body size: $F_{1,47}$ = 9.09, *P* < 0.01; species: $F_{1,47}$ = 96.10, *P* < 0.0001; interaction:

294    $F_{1,47}$ = 1.63, *P* = 0.21; Fig. 2).

295

296   Model analysis

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298   We present our results as graphical solutions owing to the complexity of the model. We

299   first consider the special case in which the maternal resource in the trophic eggs is

300   completely consumed by the offspring (i.e., $\delta = 1$). The effects of the proportion of the

301   good environment (p) on the optimal proportion of trophic eggs and on egg size are

302   depicted graphically in Fig. 3. The optimal proportion of trophic eggs relative to p is a

303   convex upward curve (Fig. 3a), and the optimal egg size decreases with p (Fig. 3b).

304   The effects of environmental predictability (q) on the optimal proportion of trophic

305   eggs and on egg size are depicted graphically in Fig. 4. The optimal proportion of trophic

306   eggs is always zero when it is not possible to predict the environment ($q = 0.5$), and it

307   increases as predictability increases (Fig. 4a).

308   The effects of the magnitude of the difference in quality between the good and poor

309   environments (k) on the optimal proportion of trophic eggs and on egg size are depicted in

310   Fig. 5. Both the proportion of trophic eggs and egg size increase with k, but the rate of

311   increase in the proportion of trophic eggs decays as k increases (Fig. 5a), whereas optimal

312   egg size increases linearly with k (Fig. 5b).

313   Finally, we consider the case that the trophic egg resource is not completely

314   consumed by the offspring ($0 \leq \delta \leq 1$). Despite the costs associated with trophic egg

315   consumption, a trophic egg strategy can evolve in heterogeneous environments (Fig. 6a).

316   In fact, the greater the difference in quality between two environments, the larger the area

317   in the parameter space where a trophic egg strategy is favoured ('trophic egg area', grey

318   and black in Fig. 6). However, trophic egg area severely decreases as investment

319   efficiency decrease, especially when the difference in quality between two environments

320   is small ($k = 1.5$, Fig. 6b).

321

322   **Discussion**

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324   Here we present three key findings in trophic egg evolution. First, intra- and interspecific

325   morphological comparisons suggest that maternal body size is at best a weak

326   morphological constraint on egg size in *H. axyridis*, which has been experimentally

327   proved to produce trophic eggs (Perry and Roitberg 2005a), and *H. yedoensis* (Fig. 1).

328   Second, we find that trophic egg-laying is expected to evolve in heterogeneous

329   environments when mothers cannot manipulate egg size plastically (Fig. 3a). Third, we

330   theoretically show that a small reduction in investment efficiency in tropic egg

331   consumption greatly reduces the likelihood of trophic egg evolution, even when cue

332   reliability is relatively high (Fig. 6). Taken together, these finding lead us to conclude that

333   maternal adaptation to highly heterogeneous environments rather than morphological

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334   constraints on egg size is a sufficient explanation for the evolution of trophic egg-laying

335   in some non-eusocial animals.

336   This is the first study to evaluate the role of morphological constraints on egg size in

337   species that produce trophic eggs. We found no significant correlation between egg size

338   and maternal body size in *H. axyridis* or *H. yedoensis* (Fig. 1), indicating that smaller

339   females can produce eggs similar in size to the eggs of larger females. Moreover, the

340   relationship between egg size and maternal body size was extremely weak in both species,

341   accounting for less than 1% of the total variation in egg size. Furthermore, *H. yedoensis*

342   females produce larger eggs than *H. axyridis* females, despite the similar maternal body

343   size in the two species (Fig. 1). A reduction in the number of ovarioles should contribute

344   to the production of larger eggs relative to maternal body size (Fig. 2). This result is

345   consistent with the previous finding that species of ladybirds with few ovarioles lay larger

346   eggs than similar-sized species with many ovarioles (Stewart et al. 1991a). These results

347   suggest that maternal body size as a morphological constraint has at best a minor role in

348   the determination of egg size in the two studied ladybird species. Recent studies of insects

349   also suggest that the importance of morphological constraints on the evolution of egg size

350   has been overemphasized (Fischer et al. 2002, Bauerfeind and Fischer 2008, Noriyuki et

351   al. 2010). Importantly, morphological constraints are particularly unlikely to exist when

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352 eggs are small relative to the size of the mother, as is the case in most insect species as

353 well as tree frogs and sharks that produce large numbers of trophic eggs. In addition, even

354 if morphological constraints prevent small females from producing eggs of optimal size,

355 such females can overcome such constraints by producing more elongated eggs

356 (Congdon and Gibbons 1987). In the subsocial bug *Adomerus triguttulus*, viable eggs are

357 more elongated than trophic eggs (Kudo et al. 2006), suggesting that the females may

358 have potential to overcome morphological constraints on egg size by changing the egg

359 morphology. Moreover, in several reptiles, smaller mothers produce elongated eggs,

360 presumably to facilitate their smooth passage out of the mother's body (Sinervo and Licht

361 1991, Clark et al. 2001, Ji et al. 2006, Rollinson and Brooks 2008). Therefore, it is

362 possible that morphological constraints may not adequately account for trophic egg

363 evolution in other animals.

364   Instead, our theoretical model showed that trophic egg provisioning to small

365 offspring is favoured in heterogeneous environments when mothers cannot manipulate

366 egg size plastically (Fig. 3). Optimal per offspring maternal investment in a poor

367 environment can also be achieved by the evolution of large eggs, without trophic

368 egg-laying, because very large offspring can survive despite variation in environmental

369 quality. As a result, in some circumstances selection favours females that consistently

370   produce large eggs. Females following this non-plastic strategy, however, are obligated to

371   invest an amount of resources in excess of the optimal value in the good environment,

372   which does not require a large amount of maternal resources. In contrast, by following a

373   trophic egg-laying strategy, females can change their per offspring maternal investment

374   even after deposition of viable eggs, suggesting that trophic egg production and

375   consumption by hatchlings allows females to flexibly adapt to a variable resource

376   environment.

377   Note that the maximum proportion of trophic eggs is predicted when $0.5 < p < 1$ (Fig.

378   3a). This result indicates that trophic egg-laying tends to be favoured when the proportion

379   of the good environment is higher than the proportion of the poor environment. This

380   result may appear counterintuitive, because we assume that mothers provision trophic

381   eggs to deal with a poor environment. However, although the large egg strategy is

382   inflexible, it can consistently achieve a high offspring survival rate even in a poor

383   environment. By contrast, a trophic egg strategy may lead to large reductions of fitness

384   and offspring survival in a poor environment if the mother incorrectly assesses the

385   environmental quality and therefore fails to provide trophic eggs to small offspring. Thus,

386   a large egg strategy, which should be a safe strategy even in a poor environment, may be

387   favoured when the proportion of poor environment is relatively high.

388   Our conclusion that evolution of trophic eggs requires a highly heterogeneous

389   environment is consistent with the empirical reports in both vertebrates and invertebrates

390   (e.g., Crump 1981, Dixon 1998). For example, in aphidophagous lacewings and ladybirds,

391   food resources are frequently and intermittently limited over time because of the

392   ephemeral nature of aphid colonies (Osawa 1992b, Hemptinne et al. 1992, Dixon 1998),

393   and they are also spatially heterogeneous in quality and quantity (Osawa 2000). In

394   sub-social animals that provide parental care to offspring even after the hatching (e.g.,

395   tree frogs, burrower bugs, and passalid beetles), as well as predatory animals without

396   effective natural enemies (e.g., sharks and ladybirds), mothers may have relatively long

397   ecological longevity and thus may experience various environmental conditions over

398   their reproductive period. Therefore, it is suggested that trophic egg provisioning may

399   function as a flexible solution for dealing with multiple habitats (Perry and Roitberg

400   2006). Because in our model we do not distinguish between spatial and temporal

401   variation, our findings are potentially applicable to diverse animal taxa producing trophic

402   eggs to cope with predictable environmental variation.

403   Our model revealed that environmental predictability enhances the likelihood that

404   trophic egg provisioning to small eggs will evolve (Fig. 4). Our result indicates that the

405   evolution of trophic egg-laying is possible in heterogeneous environments if mothers

23

406   have even a little ability to estimate the offspring's environment ($q \geq 0.5$). However, recall

407   that this result holds only when the investment efficiency of trophic egg consumption δ is

408   1 (results with $0 \leq \delta \leq 1$ are discussed below).

409   In some species with trophic egg-laying, mothers are known to evaluate

410   environment conditions that their offspring will face in several ways. For example, in tree

411   frogs, mothers adjust the number of trophic eggs based on the number of offspring (Kam

412   et al. 1998) and offspring age (Gibson and Buley 2004). In *A. triguttulus* females adjust

413   the number of trophic eggs per viable egg in response to varying resource environments

414   prior to oviposition (Kudo and Nakahira 2005). However, in a majority of trophic egg

415   laying species, the role of environmental cues in trophic egg provisioning has not been

416   examined (Perry and Roitberg 2006). In order to evaluate our model prediction that

417   environmental predictability should be necessary for evolution of trophic egg-laying (Fig.

418   4), empirical tests are required to detect maternal plasticity in trophic egg-laying.

419   Our model also demonstrated that the evolution of trophic eggs is highly sensitive to

420   the wasteful expenditure of maternal resource for trophic eggs even when environmental

421   predictability is relatively high (Fig. 6). In particular, when environmental quality does

422   not differ very much between the good and poor environments ($k = 1.5$ in Fig. 6), even a

423   small reduction of investment efficiency makes the evolution of trophic egg-laying

424 unlikely. Both nutritive parts of trophic eggs and the shells may be left uneaten by

425 offspring (Perry and Roitberg 2005a). Moreover, non-sibling conspecific individuals and

426 other predators attack trophic eggs, especially in species with no post-natal parental care

427 but also in sub-social animals (Osawa 1989, Nomakuchi et al. 2001). We suggest

428 therefore that these moderate but unavoidable costs associated with trophic egg

429 consumption may mitigate against the evolution of trophic egg-laying, thus accounting

430 for the evolution of trophic egg laying in some taxa and not others.

431   Variation in the division of maternal resources among siblings may impose both

432 costs and benefits on maternal trophic egg provisioning, although our model does not

433 explicitly consider this mechanism. Classical optimal investment theory predicts that the

434 amount of parental resource per offspring should be constant in a given environment

435 (Smith and Fretwell 1974). In real organisms, however, the amount of parental resource

436 per offspring in a brood with trophic eggs frequently varies among siblings (Osawa

437 1992a), because hatching asynchrony and trophic egg location in the clutch, for example,

438 may cause a bias in resource allocation (Osawa 1992a, Perry and Roitberg 2005a).

439 Moreover, adults that abandon their eggs presumably have little ability to control the

440 distribution of resources among offspring. Thus, it is suggested that biases in resource

441 allocation among siblings may prevent mothers from producing trophic eggs. Conversely,

442 trophic egg-laying may operate as a bet-hedging strategy by generating variation in the

443 size of offspring, the largest of which can survive in the event of unpredictable poor food

444 availability (Perry and Roitberg 2006). In support of this argument, some empirical and

445 comparative studies suggest that within-clutch variation in egg size can reflect an

446 adaptive strategy for dealing with in unpredictable environments in diverse animal taxa

447 such as frogs and fishes (Crump 1981, Einum and Fleming 2004, Marshall et al. 2008,

448 Crean and Marshall 2009). However, the bet-hedging hypothesis for trophic eggs has yet

449 to be tested against the alternative hypothesis of a single optimum in provisioning per

450 offspring. Further investigation of bet-hedging as an evolutionary mechanism promoting

451 trophic egg provisioning should be a productive area of investigation.

452   Our model results are consistent with the findings of previous theoretical studies on

453 adaptive phenotypic plasticity (Berrigan and Scheiner 2004). Specifically, models of

454 phenotypic plasticity generally show that plasticity is favoured when (1) there is

455 environmental heterogeneity (spatial or temporal), (2) there are cues that reliably predict

456 future environmental conditions, and (3) the cost of plasticity is low. Therefore, we

457 suggest that trophic egg provisioning can be regarded as one strategy of adaptive

458 phenotypic plasticity when plastic adjustment of egg size is constrained.

459   In our model, parental-offspring conflict is not taken into account: We assumed that

460   offspring cannot influence parental behaviour. Importantly, selection typically maximizes

461   maternal rather than offspring fitness, particularly in species with no post-natal parental

462   care, in which offspring counter-strategies may be less likely to evolve (Smith and

463   Fretwell 1974, Trivers 1974). However, parental-offspring conflict affects the evolution

464   of maternal reproductive strategies if offspring can counteract maternal strategies (Parker

465   et al. 2002, Perry and Roitberg 2005b). In particular, Crespi (1992) discussed

466   hypothetically the evolution of trophic eggs in the context of reduction of

467   parent-offspring conflict over sibling cannibalism. Specifically, he suggests that when

468   parent and offspring interests conflict over sibling cannibalism, mothers might adopt a

469   strategy to limit cannibalism by producing trophic eggs, which are less costly than viable

470   eggs but which provide enough energy to cause offspring to refrain from eating viable

471   siblings (Crespi 1992). This hypothesis and our predictions concerning environmental

472   heterogeneity are not necessarily mutually exclusive. Models that incorporate the

473   offspring's point of view need to be developed to predict whether Crespi's (1992)

474   argument can function as a general explanation for trophic egg evolution. However, some

475   empirical data refute the generality of the parent-offspring conflict reduction hypothesis.

476   In particular, Kudo and Nakahira (2004) explicitly rejected the hypothesis by showing in

477   careful experiments in the sub-social burrower bug that the presence or absence of trophic

478   eggs did not affect the rate of sibling cannibalism. Moreover, a cost difference between

479   trophic and viable egg production may not be common in animal species (Perry and

480   Roitberg 2006). Nevertheless, further studies are needed to identify possible differences

481   in quality between trophic and viable eggs to evaluate the parent-offspring conflict

482   reduction hypothesis.

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Figure legends

722 **Fig. 1.** Relationship between female body size and egg size (mean ± SE) by species.

723 Mean volumes of egg produced by *H. axyridis* (open circles) and *H. yedoensis* (closed

724 circles) females of a given body length.

725

726 **Fig. 2.** Relationship between female body size and number of ovarioles in *H. axyridis*

727 (open circles) and *H. yedoensis* (closed circles). Dotted and solid lines represent the linear

728 regression for *H. axyridis* and *H. yedoensis*, respectively.

729

730 **Fig. 3.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

731 of the proportion of the good environment. Parameter values used are $k = 2.0$, $q = 0.75$

732 (solid line); $k = 4.0$, $q = 0.75$ (dashed line); and $k = 2.0$, $q = 0.90$ (dotted line); where k is

733 the degree of difference between the two environments and q is environmental

734 predictability.

735

736 **Fig. 4.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

737 of environmental predictability. We did not evaluate the situation where $q < 0.5$ because it

43

738   is biologically unrealistic. Parameter values used are $k = 2.0$, $p = 0.50$ (solid line); $k = 4.0$,

739      $p = 0.50$ (dashed line); and $k = 2.0$, $p = 0.25$ (dotted line); where k is the difference

740   between the two environments and p is the proportion of the good environment.

741

742   **Fig. 5.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

743   of the difference in quality between the good and bad environments. Parameter values

744   used are $p = 0.5$, $q = 0.66$ (solid line); $p = 0.25$, $q = 0.66$ (dashed line); and $p = 0.5$, $q =$

745   0.75 (dotted line); where p is the proportion of the good environment and q is

746   environmental predictability.

747

748   **Fig. 6.** Conditions that favour a trophic egg strategy ($t > 0$) when $k = 1.5$ (black area) or k

749      $= 2.0$ (black and grey areas), depending on the investment efficiency δ (horizontal axis):

750   (a) proportion of good environment p (vertical axis), and (b) environmental predictability

751   q (vertical axis). Other parameters: (a) $q = 0.75$, (b) $p = 0.25$. In the shaded parameter area,

752   a trophic egg-laying strategy is expected to never evolve.

1 **Table**

Table 1. Relationship between environmental conditions and maternal investment

Environmental quality	Environmental predictability	Maternal strategy	Per offspring maternal investment*
Good (p)	Correct (q)	Viable eggs only	e
	Wrong ($1 - q$)	Trophic egg provisioning (if necessary)	$\{1 + \delta t/(1 - t)\}e$
Poor ($1 - p$)	Correct (q)	Trophic egg provisioning (if necessary)	$\{1 + \delta t/(1 - t)\}e$
	Wrong ($1 - q$)	Viable eggs only	e

*Model parameters e, t, and δ describe the size of viable eggs, the proportion of trophic eggs, and the investment efficiency of trophic eggs, respectively (see text for details).
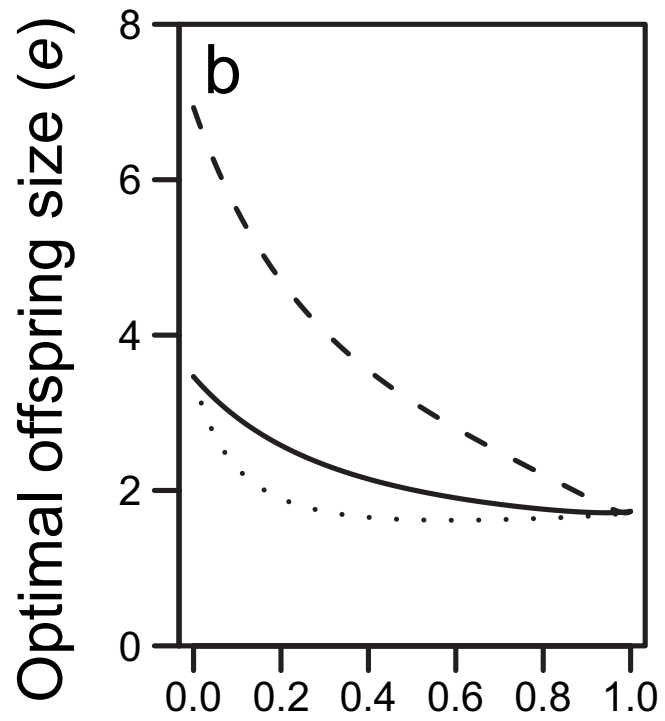
2

Fig1

Fig2

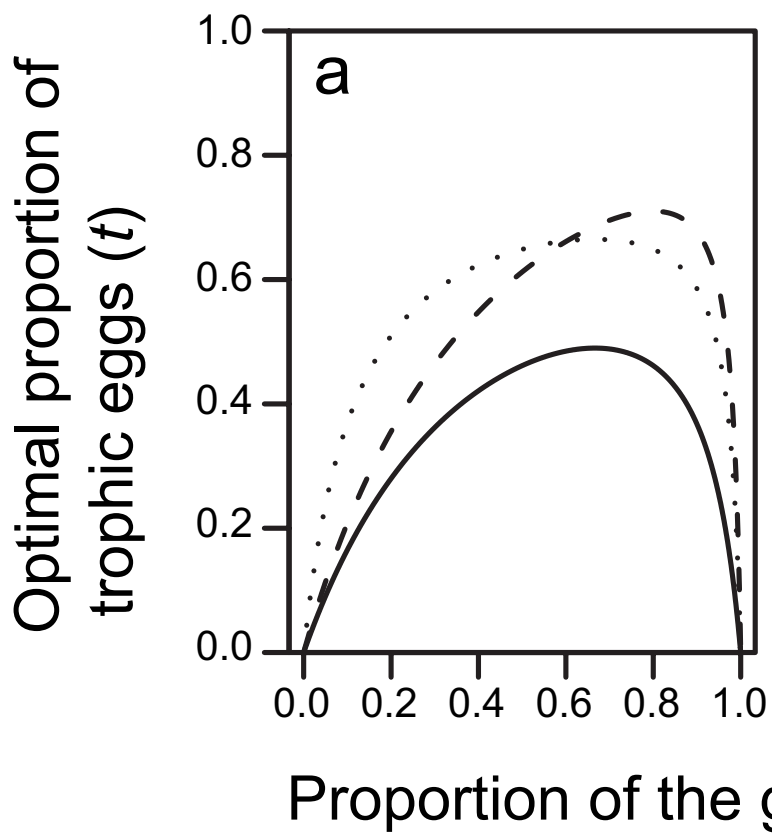O : *H. axyridis*
● : *H. yedoensis*

Ovariole number

Female body length (mm)

Figure3

Figure4

Figure5

Figure 5

a

Optimal proportion of trophic eggs (t)

1.0
0.8
0.6
0.4
0.2
0.0

b

Optimal offspring size (e)

6
5
4
3
2
1
0

Difference between the environments (k)

Figure6