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Running title: Exploration and parental effort in great tits

Authors: Morgan David*[1], Rianne Pinxten[1,2], Tine Martens[1] & Marcel Eens[1]

[1]University of Antwerp, Department of Biology-Ethology, Drie Eiken Campus, Universiteitsplein 1, 2610 Wilrijk (Antwerpen), Belgium

[2]Institute for Education and Information Sciences, Research Unit Didactica, University of Antwerp, Antwerp, Belgium.

*corresponding author (Morgan.David@gmx.fr)

E-mail addresses: Rianne Pinxten: annie.pinxten@uantwerpen.be

Tine Martens: tine.martens@uantwerpen.be

Marcel Eens: marcel.eens@uantwerpen.be

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Abstract The extended Pace-Of-Life Syndrome (POLS) hypothesis suggests that variation in

boldness-like behaviors has co-evolved with variation in life-history strategies within

populations. Yet, both theoretically-driven experiments and evidence for phenotypic

correlations between boldness-like behaviors and reproduction-related activities are scarce.

Here we test the prediction that more exploratory individuals should be willing to provide

more effort into current reproduction than less exploratory ones by investigating the

association between exploration behavior and parental effort in wild great tits (*Parus major*).

To this end, we assessed exploration behavior following a standardized assay. Then we

estimated individual willingness to provide parental effort into brood provisioning as 1)

individual increase in nest visit rate after the brood had been artificially enlarged, and 2)

individual latency to return to the nest after this manipulation. Fast male explorers were

quicker than slow explorers to return to the nest after the manipulation. Males paired with a

partner of similar exploration score - either a fast or slow female explorer - increased their

nest visit rate more than males paired with a partner of dissimilar exploration score. The

relationship between exploration and parental effort then depended on one's partner's

behavior. Our test thus provides only partial support for the extended POLS hypothesis, and

highlights the potential importance of the social environment in shaping the relationship

between boldness-like behaviors and fitness-maximising traits.

Introduction

The extended Pace-Of-Life Syndrome (POLS) hypothesis proposes that between-individual variation in boldness-like behaviors such as exploration, aggressiveness, or risk-taking, has coevolved with between-individual variation in life-history strategies (Biro and Stamps 2008; Réale et al. 2010). Life-history/behavior correlations are thus thought of as being linked with variation in individual productivity and life-history trade-offs (Biro and Stamps 2008). For instance, the extended POLS hypothesis predicts that more exploratory, active, or aggressive individuals should show lower survival prospects (Nicolaus et al. 2012; Auclair et al. 2013), but a higher metabolism (Careau et al. 2011), higher energy intake (Carter et al. 2010; David et al. 2011a), higher growth rate (Biro et al. 2014), and higher short-term reproductive success (Patterson and Schulte-Hostedde 2011).

So far, the extended POLS hypothesis has received mixed support with studies showing unexpected opposite patterns (Adriaenssens and Johnsson 2009, 2011; Smith and Blumstein 2010; David et al. 2011b; Le Galliard et al. 2013; Bridger et al. 2015), calling its generalizability into question. In addition, evidence for significant covariation between boldness-like behaviors and reproduction-related activities are scarce (Duckworth 2006; Barnett et al. 2012; Mutzel et al. 2013), while theoretically-driven tests are virtually lacking (but see Patrick and Browning 2011). For instance, the question of whether variation in boldness-like behaviors has coevolved with variation in parental care is left open. In addition, less is known about how the social environment can shape the relationship between boldness-like behaviors and fitness-maximising traits (Webster and Ward 2011). This is especially important for biparental care species where both partners of a breeding pair show common fitness prospects but also conflicts about parental duties (Lessells and McNamara 2012; Johnstone et al. 2014). Behavioral compatibility within breeding pairs has been shown to be

66 crucial for reproductive fitness in such species (Spoon et al. 2006; Schuett et al. 2011;

67 Mariette and Griffith 2012; Harris and Siefferman 2014; Mariette and Griffith 2015). Yet it

68 remains unknown whether the importance of behavioral compatibility within a pair may

69 confound and/or override the association between boldness-like behaviors and parental effort

70 expected under the extended POLS hypothesis.

71   In this study we use wild great tits (*Parus major*) to test the phenotypic relationship

72 between exploration behavior and willingness to provide provisioning effort, while taking

73 partners' exploration behavior into account. Exploration behavior has been demonstrated to

74 be heritable and repeatable in this species (e.g. Dingemanse et al. 2002), related to life-history

75 traits (e.g. Dingemanse et al. 2003, 2004) and other behaviors such as aggressiveness

76 (Verbeek et al. 1996; Mutzel et al. 2013). Exploration behavior thus reflects an ecologically-

77 relevant behavioral dimension in great tits. In the present study, willingness to provide

78 parental provisioning effort was assessed as the increase in nest visit rate following a

79 temporary artificial enlargement of brood size (Patrick and Browning 2011). To this end, we

80 monitored parental nest visits using a system of PIT-tag antennas placed at the entrance of

81 artificial nest boxes. This procedure allows to investigate individuals' willingness to provide

82 more or less effort into parental provisioning when stimulated to do so, and not genuinely the

83 investment that a bird is *a priori* expected to provide given its behavioral profile (see Fawcett

84 et al. 2013 for a more thorough discussion on the difference between evolutionary and

85 behavioural decisions). Following predictions from a recent mathematical model (Wolf et al.

86 2007), we expect fast explorers to invest more effort into current reproduction, and thus be

87 more willing to increase parental effort, than slow explorers. This is because fast explorers are

88 thought of as having lower survival prospects and thus prioritizing current over future

89 reproduction (Wolf et al. 2007; Nicolaus et al. 2012). Fast explorers should thus show a

90 higher increase in nest visit rate after the experimental brood size enlargement compared to

91 slow explorers.

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94 **Methods**

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96 Study subjects

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98 The data were collected from a suburban great tit population located on the Drie Eiken

99 Campus of the University of Antwerp, Belgium (51°9'44"N, 4°24'15"E). Circa 140 nest

100 boxes are provided for great tits to reproduce (Rivera-Gutierrez et al. 2010). Great tits can be

101 identified using metal leg rings that they receive as nestlings (day 9/10 post-hatching), or

102 using a unique combination of coloured leg rings for adults (Rivera-Gutierrez et al. 2012). For

103 all adults, one coloured ring bears a Passive Integrated Transponder (PIT) tag (IB

104 Technology, Aylesbury, UK) allowing for further bird identification using antennas (Dorset

105 Identification B.V., The Netherlands). Before the reproductive season's onset, nest boxes

106 were regularly checked for nest building indications, and then checked daily before the

107 anticipated start of egg laying up to the last egg hatches.

108   Individual parents were caught at their nest box for a short period of time when

109 feeding the chicks at day 9 post-hatching. Nestlings and unringed or untagged parents were

110 then banded and PIT-tagged. The number of chicks present inside each nest (thereafter termed

111 'brood size') was determined on day 9. On average, brood size in focal nests was 7.0±0.3

112 (SE).

115   Assessment of exploration behavior

117   Exploration behavior was assessed from the 15th to the 27th of February 2013, during the

118   winter preceding the reproductive season when the parental effort experiment was conducted.

119   Great tits were taken out the nest box within which they were sleeping at night. Birds were

120   immediately brought to an experimental room following capture, and placed alone in a cage

121   (l×w×h: 0.83×0.4×0.5m) comprising a small nest box and *ad libitum* access to mealworms,

122   sunflower seeds and water. The room temperature was 5±2°C and kept under a natural

123   light:dark cycle. On the morning following capture, birds were tested for their exploration

124   behavior in a novel environment room (l×w×h: 4.0×2.4×2.3m) comprising five artificial trees

125   (h×diameter: 1.5×0.04m) with four branches each (two at 5cm and two at 25cm below the

126   top). This is a standard procedure for assessing exploration behavior in great tits (Dingemanse

127   et al. 2002; van Overveld and Matthysen 2010; Patrick and Browning 2011; Nicolaus et al.

128   2012). A sliding door providing a direct access from the cage to the novel environment room

129   was opened by the experimenter while the lights were still off inside the latter. Then, lights

130   were turned off in the room where the cages were held and turned on in the novel

131   environment room, which stimulates birds to enter it. Individual behavior was then recorded

132   for two minutes during which the number of movements between trees and between branches

133   of the same tree was measured (thereafter referred to as 'exploration score'). Birds with high

134   exploration scores are thereafter called 'fast explorers' whereas those with low scores are

135   called 'slow explorers'. Lights from the novel environment room were turned off again, which

136 makes the bird 'freeze' and easy to catch by the experimenter. Birds were then immediately

137 taken back to and released at the place they had been caught the day before.

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140 Assessment of parental effort

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142 The amount of effort into chick provisioning was assessed using parental nest visit rate

143 (Wilkin et al. 2009; Auclair et al. 2014) following an artificial brood size enlargement

144 (Patrick and Browning 2011). In the present study we do not present results about the

145 observed relationship between exploration and nest visit rate during the pre-enlargement

146 period. A more thorough dataset using the same individuals recorded over a longer time

147 period is the subject of a future publication elsewhere. Antennas were placed at each selected

148 nest box in the afternoon of day 10 post-hatching. Focal nest boxes were selected on the basis

149 that, when possible, both parents were PIT-tagged and other nest boxes from which to take

150 chicks of the same age for the artificial enlargement were available. Overall, we used 14 nest

151 boxes where both parents were tested for exploration behavior, four nest boxes for which only

152 the male was exploration-tested, two nest boxes for which only the female was exploration-

153 tested, and one nest box for which neither parents were exploration-tested. This latter nest box

154 was obviously only used in analyses that did not involve exploration scores (i.e. between-

155 period change in nest visit rate). Overall, 34 birds were tested for exploration behavior, while

156 eight were not. However, provisioning behavior was recorded for all of them. Each setup

157 consisted of a box (43×33×9cm) placed on the ground close to the tree to which the nest box

158 was attached. It contained all the electronic devices, including data logger, the battery and the

159 USB stick on which data about nest visits were stored. This box was linked with a thin wire to

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160   a circular antenna with cycles of 10 detections per second, placed inside the nest box and

161   fitted with the entrance hole. The actual antenna replaced a dummy antenna that had been set

162   before the start of the breeding season in order for birds to familiarize with it. The installation

163   of the whole antenna system by the experimenter (MD) was not to last more than a couple of

164   minutes thus minimizing disturbance at the nest. The artificial brood size enlargement

165   occurred on the morning of day 13 post-hatching, when chicks' feeding frequency peaks in

166   great tits (Barba et al. 2009).

167   On day 13 post-hatching, nest boxes which were not included further in the

168   experiment and for which chicks were of the same age as those of the monitored focal nest

169   boxes were selected. The experimenter (MD) collected two chicks from these nest boxes.

170   These were then carried and added to a focal nest (enlargement's starting time ± SE:

171   9:23am±4 min.). They remained in the focal nest box for 2:30 hours after what they were

172   placed back in their original nest. The antenna setup was removed from the focal nest box

173   shortly afterwards.

174   The brood size manipulation caused parents to temporarily fly away from the nest box.

175   We considered the time delay to return to the nest box after the manipulation as an indication

176   of a bird's willingness to provide parental effort despite a potential hazard. Individuals

177   returning faster to the nest box after the manipulation are thus thought of as being more

178   willing to provide parental effort than individuals returning later.

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181   Data processing

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183   We computed a similarity index indicating to what extent both partners of a given breeding

184   pair are similar in terms of exploration behavior, following the formula:

$$Similarity\ index = |female\ exploration\ score - male\ exploration\ score|$$

185   In our sample, similarity indices range from 3 (pairs of individuals with highly similar

186   exploration scores) to 26 (pairs of individuals with highly dissimilar exploration scores).

187   Nest visit rate was computed as the number of minutes per hour that an individual was

188   detected at the nest divided by the number of minutes within an hour (i.e. 60). This method

189   has previously been used in studies of great tits' provisioning behavior using the same

190   antennas' apparatus (Wilkin et al. 2009; Patrick and Browning 2011), and is considered to

191   reliably reflect chicks' feeding rate (Wilkin et al. 2009). To compute the difference in nest

192   visit rate before versus after brood size enlargement (respectively pre- and post-enlargement

193   period), thus controlling for between-pair initial differences in nest visit rate, we quantified

194   nest visit rate during 2:15h before and after the manipulation. The measurement of nest visit

195   rate after brood size enlargement started 15min after the manipulation to allow parents to

196   recover from the associated disturbance (see Limbourg et al. 2013). We chose this duration as

197   birds were re-detected by the antenna after a median delay of 7.5 minutes (interquartile range:

198   [3,14]). Eighty-eight percent of the birds (37 out of 42) were re-detected by the antenna within

199   the 15min-period following the manipulation. Analyses conducted only with these individuals

200   that were re-detected by the antenna within the 15min-period substantially yield the same

201   results (not shown). For each parent we recorded the time delay (in number of minutes) it took

202   to come back to its nest after the manipulation as a measure of willingness to provide parental

203   effort. The relative change in nest visit rate following brood size enlargement was computed

204   for each individual as follows:

Relative change in nest visit rate

$$= \frac{(Nest\ visit\ rate\ during\ the\ post\ enlargement\ period - Nest\ visit\ rate\ during\ the\ pre\ enlargement\ period)}{Nest\ visit\ rate\ during\ the\ pre\ enlargement\ period}$$

205   The computation of this index indeed allows for a control of potential initial differences in

206   nest visit rate between pairs. Also it enables us to reduce the number of predictors in our

207   models, thus diminishing the risk of overloading our models with many parameters given our

208   small sample size. The relative change in nest visit rate was log-transformed for every

209   analysis so as to reach normality (Shapiro test: W=0.96, *P*=0.16) and be bounded by minus

210   and plus infinity rather than -1 and plus infinity otherwise.

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213   Statistical Analyses

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215   Statistical models were built to, first, investigate any potential link between time delay to

216   return to the nest after the manipulation and exploration behavior; second, determine whether

217   brood size enlargement was efficient at stimulating higher nest visit rates; third, examine

218   whether fast explorers increased their nest visit rate more following brood size enlargement

219   than slow explorers, and fourth, test whether the increase in nest visit rate was linked to the

220   similarity in exploration behavior between members of a pair. In the present paper we did not

221   intend to test the relationship between brood size and exploration, which will be the subject of

222   another publication elsewhere with a more thorough dataset. However we added the variable

223   'brood size' as a fixed effect in most of our models. Models were, otherwise stated, computed

224   using the 'glmer' command from the 'lme4' R package (Bates et al. 2014). We proceeded to

225   stepwise backward deletion of the least significant term until only significant variables

226 remained in the model with a significance threshold set at $P=0.05$. We provided Cliff's δ

227 (Cliff 1996; Torchiano 2014), Pearson's (r) and Spearman's (r_s) correlation coefficients as

228 effect sizes with the associated sample size (Nakagawa and Cuthill 2007).

229   In a first generalized linear mixed model (GLMM) we set time delay (i.e. number of

230 minutes between the manipulation and bird detection at the nest) as a response variable.

231 Predictors were brood size and the triple interaction between sex, exploration score and

232 partner's exploration score. 'Pair' was added as a random intercept variable to account for the

233 non-independence of females and males' behavior within pairs. We set the model error

234 structure to negative binomial as our response variable showed signs of overdispersion. We

235 therefore used the 'glmmADMB' R package to analyze this model (Fournier et al. 2012;

236 Skaug et al. 2014).

237   In a second GLMM we set nest visit rate as a response variable. To this end we used

238 the *cbind* command including both the number of minutes per hour that a given bird had been

239 detected by the antenna and the number of minutes per hour that the bird had not been

240 detected by the antenna (see Crawley 2007). Brood size and the interaction between period

241 (pre- and post-enlargement) and sex were added as predictors. In order to control for the non-

242 independence of males and females' behavior within the same pair, and for the repeated

243 measures of the same individual across the two periods, individual ID, nested within pair, was

244 set as a random intercept factor. We also tested this model with 'period' added as a random

245 slope factor, as recommended by Schielzeth and Forstmeier (2009). The error structure was

246 set to binomial.

247   Using correlation analyses, we investigated the potential relationship between nest

248 visit rate before brood size enlargement on day 13 and the change in nest visit rate following

249 brood size enlargement following Tu and Gilthorpe's (2007) standardized procedure (David et

250 al. 2012). This is to test whether the increase in provisioning effort following brood size

251   enlargement depends on the amount of provisioning provided beforehand. We may indeed

252   expect individuals provisioning at a high rate to be less capable of increasing their investment

253   following brood size enlargement.

254   In a third GLMM we set the log-transformed relative change in nest visit rate (see

255   above) as the response variable. Brood size and the interaction between exploration score,

256   partner's exploration score and sex were added as predictors. To account for the non-

257   independence of males and females' behavior within the same pair, we added 'pair' as a

258   random intercept variable. The error structure was set to Gaussian. We could not add one's

259   partner relative change in nest visit rate as a predictor in this model as, due to its very random

260   effect structure, it would have prevented it from converging properly. We have thus tested the

261   correlation between relative change in nest visit rate and one's partner's aside.

262   In a fourth GLMM we tested the relationship between the relative change in nest visit

263   rate and the similarity index (see above). The log-transformed relative change in nest visit rate

264   was defined as the response variable, and similarity index was set as a predictor. We added

265   'pair' as a random intercept variable, and set the model error structure to Gaussian.

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267

268   **Results**

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270   Fast explorers returned quicker to the nest after the manipulation

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272   Time delay to come back to the nest after brood size enlargement was affected by the

273   interaction between sex and exploration score (z=-1.96, P=0.050; Table 1) (females:

274   Spearman's $r_s(14)=-0.05$, 95% Confidence Interval (CI)$=(-0.73,0.60)$; males: $r_s(14)=-0.67$,

275   95%CI$=(-0.95,-0.18)$; Fig. 1, Table 1), and brood size (regression's slope estimate $b\pm SE=-$

276   0.22 ± 0.11, $P=0.047$, $r_s(28)=-0.46$, 95%CI$=(-0.73,-0.12)$; Table 1), but not by partner's

277   exploration score ($b\pm SE= -0.03\pm0.02$, $P=0.15$, $r_s(28)=-0.20$, 95%CI$=(-0.55,0.18)$; Table 1).

278   Fast male explorers were quicker to return to the nest after the manipulation. No other

279   interaction terms were found to be significant (Table 1). Both partners' time delay to return to

280   the nestbox were positively correlated ($r_s(21)=0.47$, 95%CI$=(0.07,0.78)$, $P=0.025$).

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283   Brood size enlargement triggers higher nest visit rate

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285   Nest visit rate significantly increased between the pre-enlargement and the post-enlargement

286   period (pre-enlargement period: rate$\pm SE=0.35\pm0.02$; post-enlargement period:

287   rate$\pm SE=0.39\pm0.03$; $b\pm SE=0.18\pm0.04$, Cliff's $\delta=0.23$, 95%CI$=(-0.14,0.36)$; $\chi^2=19.85$, df=1,

288     $P<0.0001$; Fig. 2), irrespective of sex (interaction sex $\times$ period: $\chi^2=0.77$, df=1, $P=0.38$).

289   However, the effect of the period no longer remained significant when 'period' was added as

290   a random slope factor in the model ($b\pm SE=0.15\pm0.09$; $\chi^2=2.54$, df=1, $P=0.11$). Brood size had

291   a significant positive effect on nest visit rate ($b\pm SE= 0.30\pm0.08$, $\chi^2=11.37$, df=1, $P<0.001$;

292     $r_s(84)=0.48$, 95%CI$=(0.28,0.64)$). Brood size enlargement was efficient at stimulating parents

293   to increase their provisioning behavior. The change in nest visit rate following brood size

294   enlargement was not related to nest visit rate before the manipulation ($r(42)=-0.18$, 95%CI$=(-$

295     $0.46,0.14)$, $P=0.27$; see methods) nor was it significantly predicted by time delay to come

296   back to the nest after the manipulation ($r_s(42)=-0.05$, 95%CI$=(-0.36,0.27)$, $P=0.78$).

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299   Partners' combined exploration scores influence parental effort

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301   The relative change in nest visit rate was significantly affected by the interaction between sex,

302   exploration score and one's partner exploration score (χ^2=5.36, df=1, P=0.021), but not by

303   brood size (b±SE=0.04±0.06, χ^2=0.86, df=1, P=0.35). Taking each sex separately, the

304   interaction between exploration score and one's partner exploration score was significant in

305   males (t_{10}=3.48, P=0.006; Fig. 3a) but not in females (t_{10}=1.21, P=0.25; Fig. 3b). Males

306   paired with a female of similar exploration score increased their nest visit rate more than

307   males paired with a female of dissimilar exploration score (Fig. 3a). In females, the relative

308   change in nest visit rate was not related to exploration score (b±SE=0.01±0.01, t_{11}=0.91,

309   P=0.38) nor partner's exploration score (b±SE=0.01±0.01, t_{12}=0.83, P=0.42). However, the

310   similarity index was negatively linked to the relative change in nest visit rate in females

311   (b±SE=-0.02±0.01, t_{12}=-2.47, P=0.030, r_s(14)=-0.59, 95%CI=(-0.80,-0.27); Fig. 4), as well as

312   in males (b±SE=-0.04±0.01, t_{12}=-2.89, P=0.014, r_s(14)=-0.60, 95%CI=(-0.88,-0.10); Fig. 4),

313   indicating that effort into provisioning indeed was higher in pairs of birds with similar

314   exploration behavior.

315   Individual relative change in nest visit rate was found to be positively and significantly

316   related to one's partner's (r(21)=0.46, 95%CI=(0.04,0.74), P=0.033; Fig. 5).

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318

319   **Discussion**

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321   The extended POLS hypothesis provides clear predictions about the expected relationship

322   between within-population variation in boldness-like behaviors and life-history traits. In the

323   present paper we conducted a test of the relationship between exploration behavior and

324   willingness to provide parental effort in a wild great tit population. Below we discuss the

325   scope and limitations of our findings and their relevance and implication in relationship with

326   theory.

327   The artificial enlargement of brood size was designed to stimulate individuals to put

328   more effort into chicks provisioning than they would have normally done. Also, the

329   computation of the relative increase in nest visit rate controlled for potential initial between-

330   pair differences in provisioning rate, providing a 'control' measure to the nest visit rate as

331   quantified after the enlargement. Despite this control, it remains possible that the relative

332   increase in nest visit rate may have been influenced by any natural dynamic daily pattern of

333   parental provisioning, something that we were not able to control in this experiment.

334   However, if provisioning rate has been shown to peak at dawn and dusk in great tits (Patrick

335   and Browning 2011), the daily pattern of provisioning was shown not to differ between

336   individuals with varying exploration behavior (Patrick and Browning 2011). We thus think

337   that it is unlikely that the observed relationship between the relative increase in nest visit rate

338   and exploration was the mere outcome of variation in daily patterns of provisioning. We

339   believe that the brood size manipulation was appropriate to identify which individuals and to

340   what extent they were willing to put more effort into parental duties, and thus to place more

341   weight onto current reproduction than others.

342   Nest visit rate was computed from the proportion of minutes per hour that a bird was

343   detected by the antenna placed at the nest entrance (Patrick and Browning 2011). Although

344   this method does not give an exact measure of how much time parents spend at the nest, or

345   any clue about the quantity and quality of food brought to the chicks, it has already been used

346 in previous studies (Patrick and Browning 2011) and shown to reliably reflect chicks'

347 provisioning rate (Wilkin et al. 2009). We are thus confident that our estimate of nest visit

348 rate is a reliable proxy for parental provisioning rate, and possibly for the amount of food

349 brought to the offspring. The possibility yet remains that parents visiting more also bring

350 lower-quality food than others. Unfortunately this issue cannot be investigated using the

351 present experimental procedures and would deserve further research.

352   The average increase in nest visit rate between the two periods was found to be rather

353 low (4%), and even non-significant when 'period' was added as a random slope factor in the

354 model, providing at best only little evidence that birds increased their provisioning rate after

355 the brood size enlargement. Also, several individuals did not increase but decreased or kept

356 their nest visit rate stable across the two periods (see Fig. 2). The possibility exists that some

357 individuals may simply have not responded to the manipulation for several reasons: on the

358 one hand, they may not have had sufficient time to detect and respond to the manipulation

359 (two hours and fifteen minutes). On the other hand, some individuals may not have responded

360 to the enlargement because they had already reached their maximum level of effort into

361 provisioning before the manipulation. However, we did not find any significant correlation

362 between nest visit rate before the manipulation and the increase resulting from the

363 manipulation, which makes the latter possibility unlikely. It may also be that some birds did

364 not respond to the manipulation because their partner responded sufficiently (the reproductive

365 compensation hypothesis, Gowaty et al. 2007), but we think that this also is unlikely given the

366 positive relationship we found between an individual's relative change in nest visit rate and its

367 partner's (Hunt and Simmons 2002), which on the contrary is more indicative of a social

368 facilitation phenomenon. Further studies would be needed to understand why some birds are

369 responsive and some are not.

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372   The importance of the social environment when testing the POLS hypothesis

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374   In accordance with the extended POLS hypothesis, we found that fast explorers were quicker

375   to come back to the nest after brood size enlargement than slow explorers, a finding

376   reminiscent of a recent comparable result during the incubation stage in the same species

377   (Cole and Quinn 2014). In addition, the relative change in nest visit rate was influenced by the

378   interaction between an individual's exploration score and its partner's, at least in males.

379   Individuals within assorted pairs for exploration scores (fast – fast explorers, and slow – slow

380   explorers) showed a higher increase in nest visit rate than individuals within non-assorted

381   pairs, irrespective of their own exploration behavior. In females we detected no effect of

382   exploration behavior on the relative increase in nest visit rate. Yet, based on the correlation

383   between the similarity index and the relative increase in nest visit rate, females paired with a

384   male of similar exploration behavior were found to be more likely to increase their nest visit

385   rate than in dissimilar pairs. We believe that this discrepancy may come from our small

386   sample size and a lack of statistical power in the first mentioned linear model. We indeed

387   acknowledge that the sample size of our study is pretty low and further studies would be

388   needed to test the generalizability of these results. That said, our findings provide only partial

389   support for the extended POLS hypothesis which predicts that fast explorers should, all else

390   being equal, provide more effort into current reproduction than slow explorers. Indeed, in the

391   present study, fast explorers provisioned their brood more when paired with a fast partner than

392   when paired with a slow one. Conversely, slow explorers provisioned their offspring less

393   when paired with a fast explorer, than when paired with a slow explorer. The importance of

394   combined behavioral types within breeding pairs is reminiscent of previous findings that

395   assortment for behavioral traits affects reproductive fitness in pairs of great tits (Dingemanse

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396 et al. 2004), zebra finches (*Taeniopygia guttata*) (Schuett et al. 2011), Steller's jays

397 (*Cyanocitta stelleri*) (Gabriel and Black 2012), eastern bluebirds (*Sialia Sialis*) (Harris and

398 Siefferman 2014), and guppies (*Poecilia reticulata*) (Ariyomo and Watt 2014). The functional

399 consequences and the reasons why it may be optimal for individuals to breed with partners of

400 similar behavioral type remain unclear so far (Kralj-Fišer et al. 2013). Specific combinations

401 of behavioral types within breeding pairs may affect brood provisioning efficiency (Mutzel et

402 al. 2013), for instance through provisioning synchronization (Mariette and Griffith 2012; see

403 van Rooij and Griffith 2013). The extent to which (i) pairs of partners with similar exploration

404 behavior are better synchronized, and (ii) better synchronization leads to higher reproductive

405 success remains to be determined. The positive correlation between both partners' time delay

406 to return to the nest and between both partners' relative change in nest visit rate, while

407 confirming previous studies (Hinde 2006; Westneat et al. 2011), also suggests that such

408 synchronization phenomenon could be at work in our study. Indeed, it may be that social

409 facilitation leads partners to change their nest visit rate to the same extent and that any sort of

410 social facilitation effect is more salient when partners are of similar exploration behavior.

411 However, this interpretation remains speculative and more work is needed to disentangle the

412 complex interplay among partners' behavioral types, provisioning behavior and reproductive

413 success (Mutzel et al. 2013).

414   The interaction between individual exploration score and partner's exploration score in

415 determining brood provisioning effort suggests the importance of the social environment in

416 shaping the relationship between boldness-like behaviors and reproduction-related activities,

417 and fitness-maximising traits in general (Bergmüller and Taborsky 2010; Webster and Ward

418 2011). It is especially important as an individual's reproductive success greatly depends on its

419 partner's investment into breeding in biparental care species. Testing for a positive

420 relationship between boldness-like behaviors and reproductive effort may thus become

421   inconclusive because of the social environment's influence (in the present case one's partner

422   behavior). In particular, the importance of behavioral compatibility for reproductive fitness

423   within breeding pairs (Spoon et al. 2006) may override the positive association between

424   exploration and provisioning effort. Boldness-like behaviors are known to be substantially

425   affected by the social environment (Mainwaring et al. 2011; Webster and Ward 2011). We

426   believe that it would be elusive to ignore its influence (be it a constraint or a facilitator) when

427   testing predictions of the extended POLS hypothesis in social species, especially in a

428   reproductive context where both partner's fitness prospects converge. Taking the social

429   environment into account should involve studying pairing patterns with respect to boldness-

430   like behaviors, and determining the functional relationships between boldness-like traits and

431   fitness (i.e. questioning what the factors mediating the link between both are) (Patrick and

432   Browning 2011; Mutzel et al. 2013).

433

434

435   POLS hypothesis and the multidimensionality of reproductive investment

436

437   Overall, our results provide, at best, partial support for the extended POLS hypothesis with

438   possible sex effects. Our findings differ from a previous correlational study in wild blue tits

439   (*Cyanistes caeruleus*) which showed a positive relationship between exploration behavior and

440   brood provisioning rate in females only (Mutzel et al. 2013). Our results also differ from

441   another study using a similar experimental design that did not identify any significant link

442   between exploration and brood provisioning in great tits (Patrick and Browning 2011). The

443   possibility remains that various wild great tit populations exhibit different patterns of

444   behavioral correlations depending on the specific selective pressures or the constraints they

445 face, or on their particular life-histories (Adriaenssens and Johnsson 2009; Patrick and

446 Browning 2011). Finally, in western bluebirds (*Sialia mexicana*), male provisioning rate has

447 been found to be negatively related to aggressiveness (Duckworth 2006). In this latter study,

448 the direction of the relationship between parental effort and boldness-like traits goes against

449 the extended POLS hypothesis' predictions. However, it is noteworthy that aggressiveness

450 may be related to several functional behaviors that a given male may have to trade-off against

451 one another. In the case of western bluebirds for example, more aggressive males spend more

452 time defending their nest against potential predators and competitors (Duckworth 2006). This

453 can reasonably be considered as investment into a reproduction-related activity as a male's

454 reproductive fitness likely depends on keeping the nest safe away from potential hazards. This

455 is because investment into current reproduction may concern various dimensions of

456 reproductive behavior, such as nest defence (Hollander et al. 2008), extra-pair sexual behavior

457 (Patrick et al. 2012), or parental care (Barnett et al. 2012), that the link between boldness-like

458 behavioral variation and brood provisioning effort may differ among populations or species.

459 This possibility argues in favour of the necessity to confirm, generalize, and extend the

460 present findings to other species and/or other populations of the same species. This is

461 important in order to refine the extended POLS hypothesis, and understand unexpected

462 associations between variables (David et al. 2011b; Adriaenssens and Johnsson 2011). Also,

463 we encourage the simultaneous study of multiple behavioral dimensions within the same

464 functional context (e.g. in a reproductive context: signaling, parenting, and so on…) insofar as

465 these various dimensions may not be all maximised at the same time and may be traded-off

466 against one another (Fig. 6). These trade-offs may contribute to confound the relationships

467 between boldness-like behaviors and reproduction-related activities expected under the

468 extended POLS hypothesis' framework.

469

470

471 Conclusion

472

473 To conclude, our findings indicate that both an individual's behavioral type and its partner's

474 can be critical in its decision to provide more or less effort into brood provisioning. This

475 interaction is supposed to have a great impact on the relationship between boldness-like

476 behaviors and reproduction-related activities, and thus on the testing of the extended POLS

477 hypothesis' predictions. Future studies should then carefully consider the social environment

478 (Bergmüller and Taborsky 2010) when testing predictions of the extended POLS hypothesis.

479 Further investigations are also needed to integrate various reproduction-related activities

480 together into a single test of the extended POLS hypothesis.

481

490

491

492 **Ethical standards**

493

494   This study was approved by the ethical committee of the University of Antwerp (ID

495   number 2011-31) and it was performed in accordance with Belgian and Flemish laws. The

496   Belgian Royal Institute for Natural Sciences (Koninklijk Belgisch Instituut voor

497   Natuurwetenschappen) provided ringing licences for authors and technical personnel.

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499

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645   **Caption for table**

646

647   **Table 1**

648   Results of the models testing the relationship between the time delay taken by birds to return

649   to the nest after brood size enlargement, and sex, brood size, exploration score, and partner's

650   exploration score. Significant terms are highlighted in bold

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Captions for figures

Fig. 1. Influence of exploration score on time delay to return to the nest (in number of

minutes) after brood size enlargement

Fig. 2. Variation in nest visit rate between pre- and post-brood size enlargement periods at

day 13. Each line represents a single individual. Females are represented in red (light lines)

and males in blue (dark lines). The dashed line is the sample average. Note that the difference

between the two periods no longer remains significant when 'period' is set as a random slope

factor in the model

Fig. 3. Relationship between individual exploration score, partner's exploration score and

relative change in nest visit rate in males (a) and females (b). Regression planes represent the

models' predictions. The relative change in nest visit rate was log-transformed (see methods)

Fig. 4. Negative relationship between the relative change in nest visit rate and the similarity

index. Individuals increased their nest visit rate after brood size enlargement more when

paired with a more similar partner in terms of exploration behavior. The relative change in

nest visit rate was log-transformed (see methods)

Fig. 5. Positive relationship between an individual's relative change in nest visit rate and its

partner's. Each point corresponds to both partners of a given breeding pair. The relative

change in nest visit rate was log-transformed (see methods)

678

679 **Fig. 6.** Integration of various reproduction-related behaviors into a single test of the extended

680 POLS hypothesis. Insofar as different components of reproduction can be related with one

681 another, the overall individual effort into reproduction can be assessed by taking the residuals

682 of the regression from the effort provided into one component on the other (Principal

683 components analyses may be considered when more than two components are involved).

684 According to the extended POLS hypothesis, proactive individuals should overall invest more

685 into reproduction-related activities than reactive individuals. In this hypothetical example of a

686 trade-off between parenting and mating effort, proactive individuals are then on average

687 expected to have higher residual values than reactives

688

689

690 **Table 1**

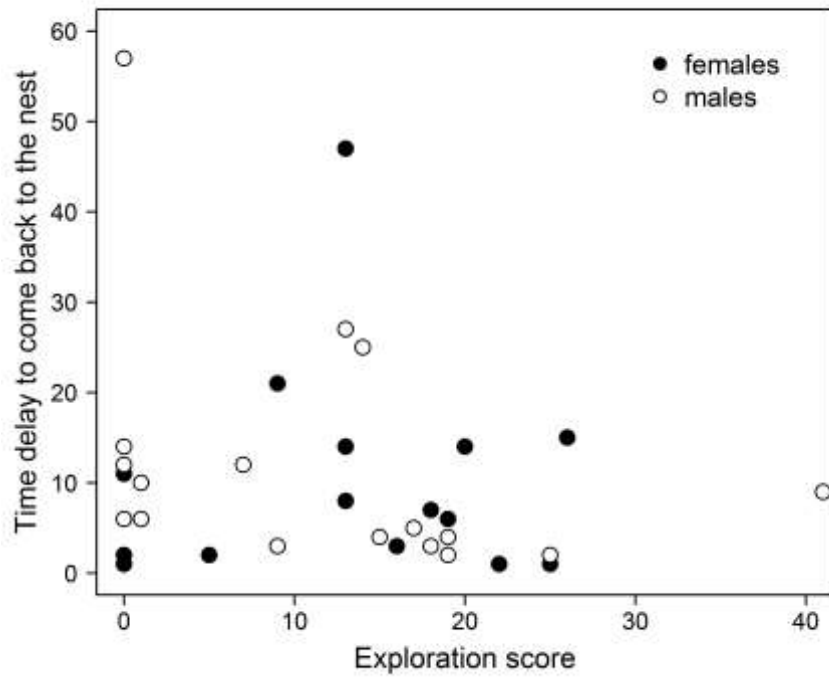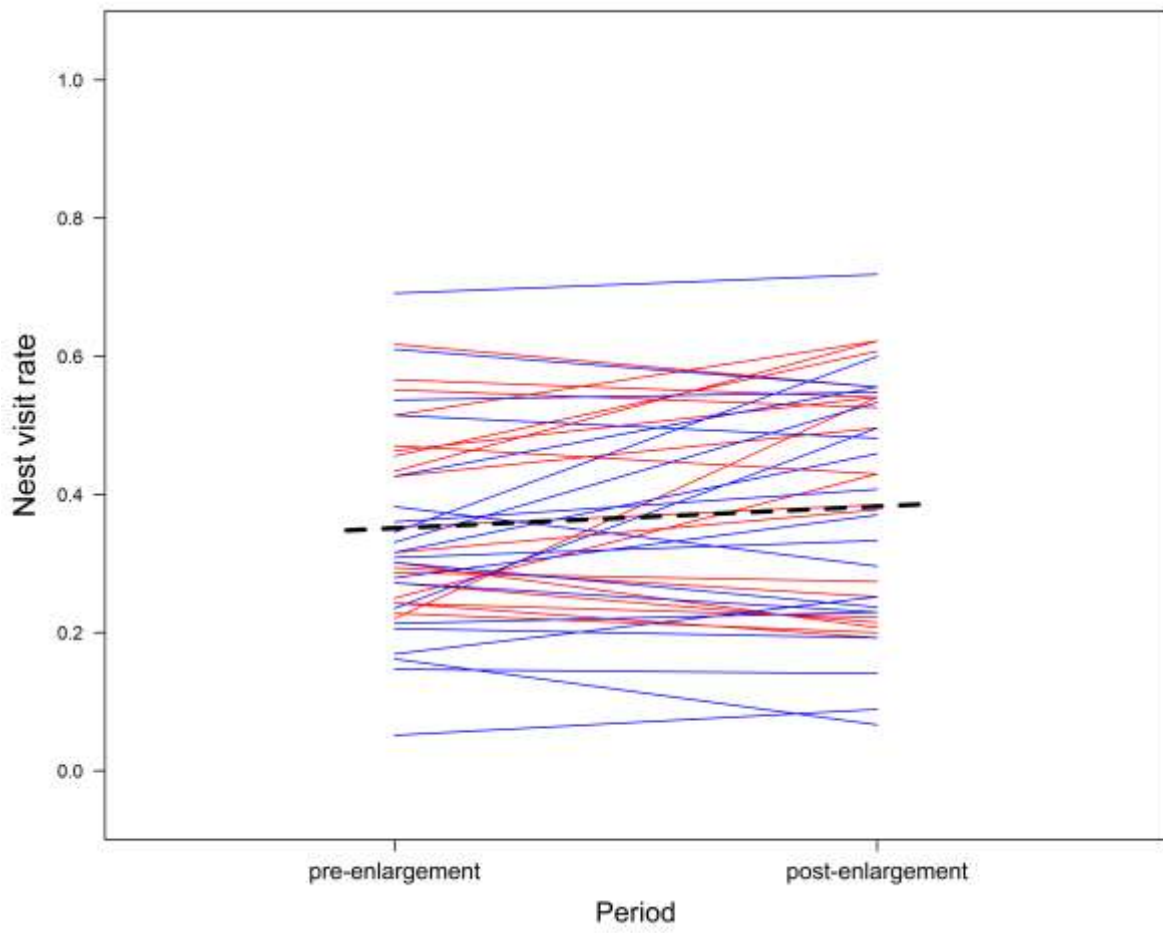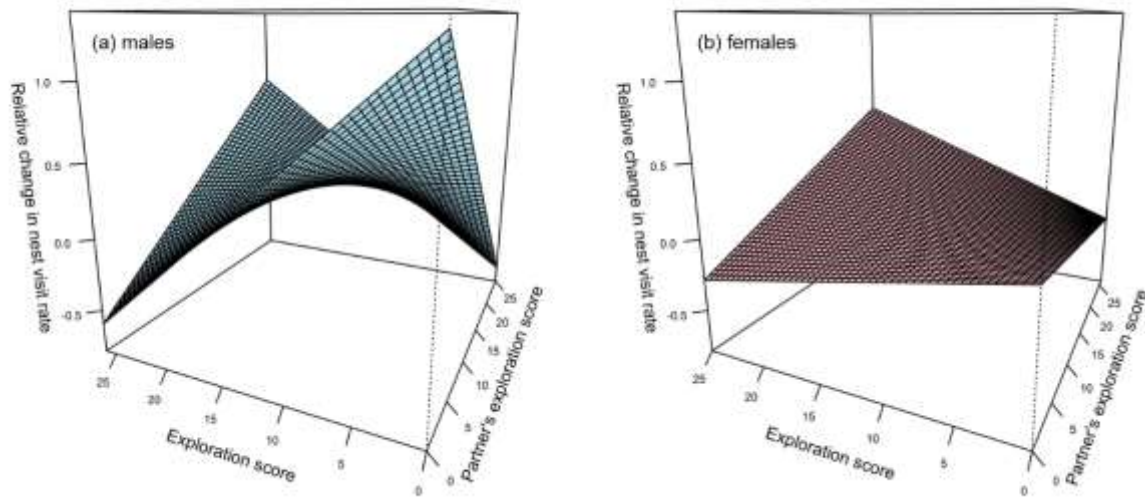|	Time delay to return to the nest	
	z	P
Brood size	**-1.98**	**0.047**
Partner's exploration score	-1.46	0.15
Sex × exploration score	**2.39**	**0.050**
Sex × Partner's exploration score	1.13	0.26
Exploration score × Partner's exploration score	0.77	0.44
Sex × Exploration score × Partner's exploration score	-1.96	0.73

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694　**Figure 1**

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698   **Figure 2**

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701 **Figure 3**
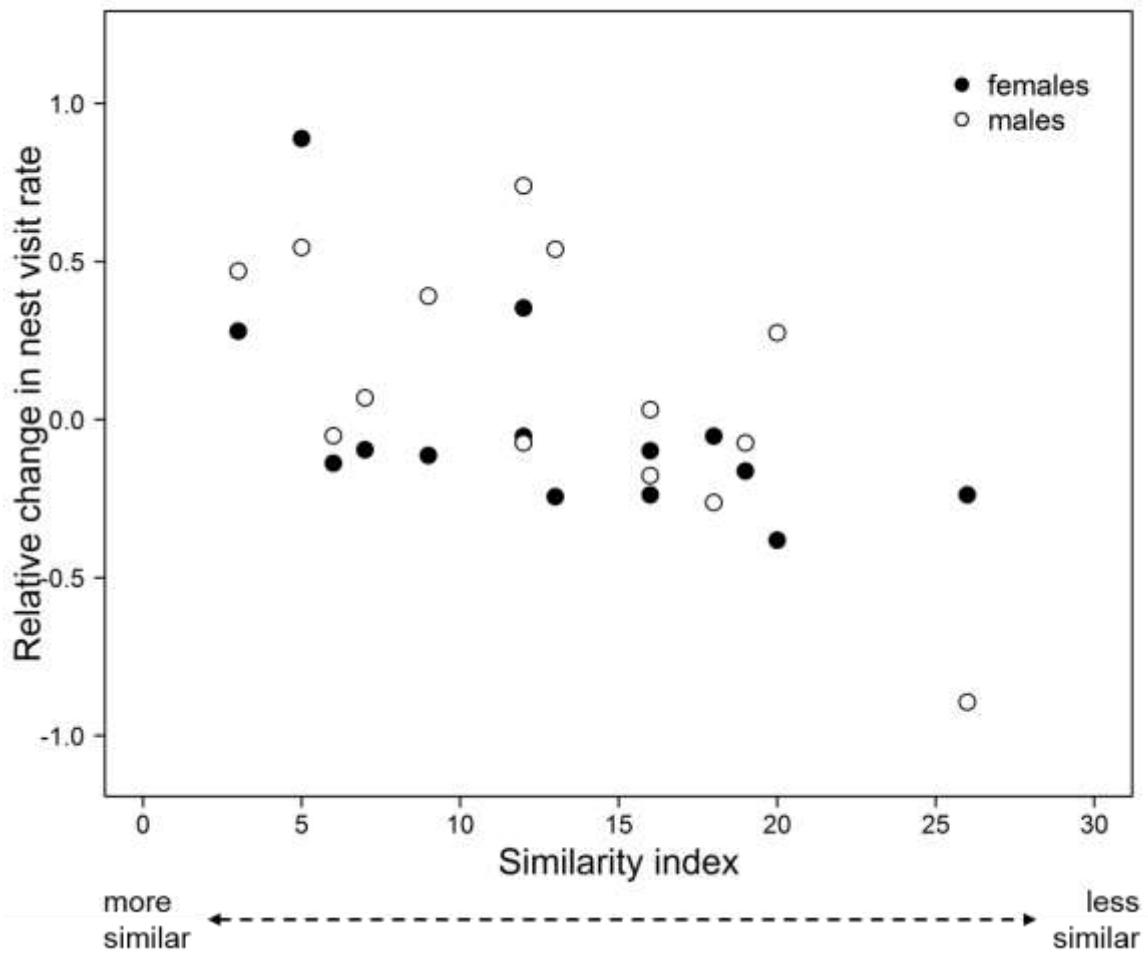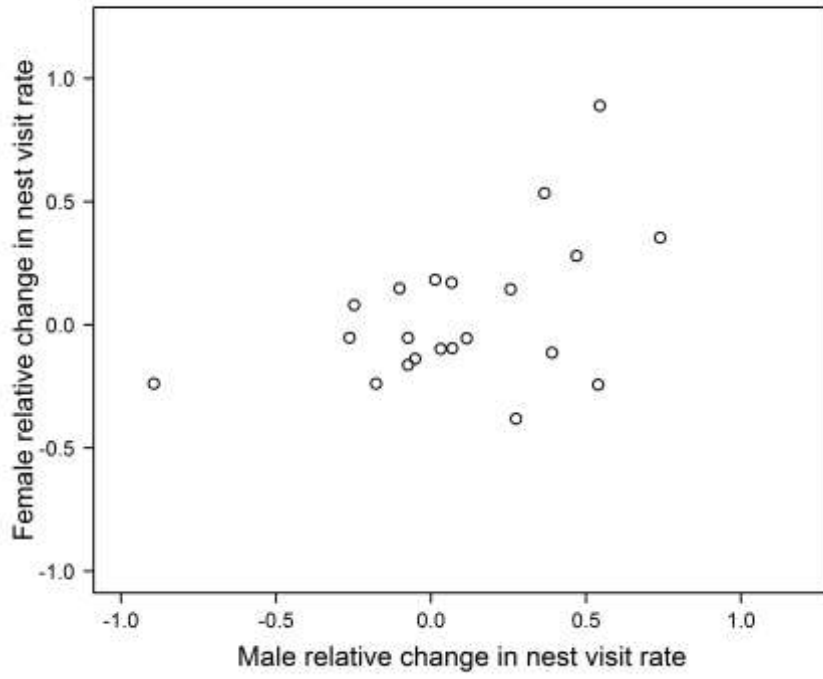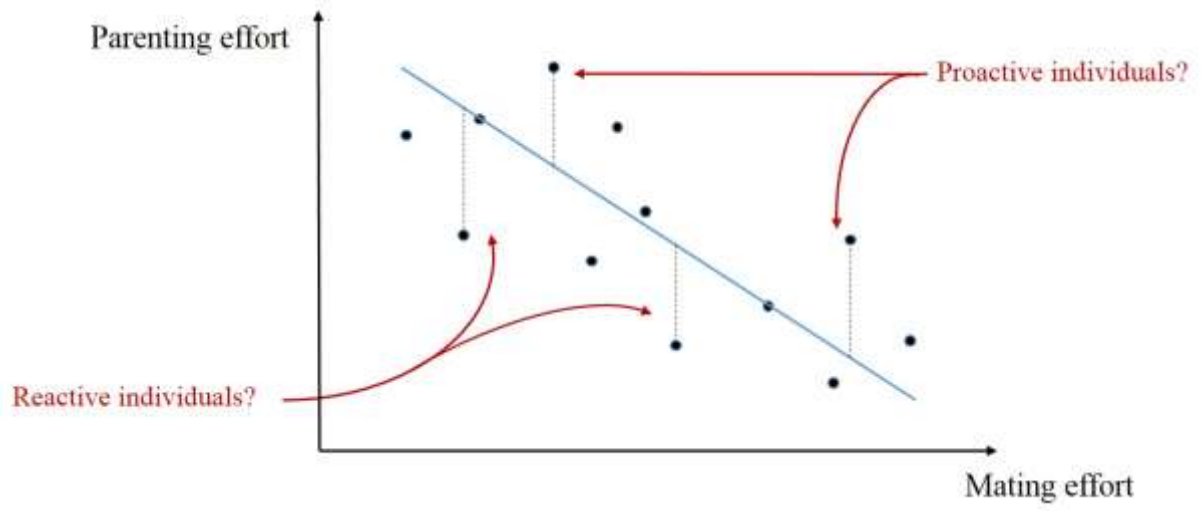
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706   **Figure 4**

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710   **Figure 5**

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714 **Figure 6**

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