

Exploration behavior and parental effort in wild great tits: partners matter

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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-maximizing traits.

Keywords Brood size manipulation · Pace-of-life · *Parus major* · POLS · Parental care · PIT tags · Provisioning · Partner's compatibility

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

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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 on 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-maximizing 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 crucial for reproductive fitness in such species (Spoon et al. 2006; Schuett et al. 2011; Mariette and Griffith 2012, 2015; Harris and Siefferman 2014), yet it remains unknown whether the importance of behavioral compatibility within a pair may confound and/or override the association between boldness-like behaviors and parental effort expected under the extended POLS hypothesis.

In this study, we use wild great tits (*Parus major*) to test the phenotypic relationship between exploration behavior and willingness to provide provisioning effort, while taking partners' exploration behavior into account. Exploration behavior has been demonstrated to be heritable and repeatable in this species (e.g., Dingemanse et al. 2002), related to life-history traits (e.g., Dingemanse et al. 2003, 2004) and other behaviors such as aggressiveness (Verbeek et al. 1996; Mutzel et al. 2013). Exploration behavior thus reflects an ecologically relevant behavioral dimension in great tits. In the present study, willingness to provide parental provisioning effort was assessed as the increase in nest visit rate following a temporary artificial enlargement of brood size (Patrick and Browning 2011). To this end, we monitored parental nest visits using a system of PIT-tag antennas placed at the entrance of artificial nestboxes. This procedure allows to investigate individuals' willingness to provide more or less effort into parental provisioning when stimulated to do so, and not genuinely the investment that a bird is a priori expected to provide given its behavioral profile (see Fawcett et al. (2013) for a more thorough discussion on the difference between evolutionary and behavioral decisions). Following the predictions from a recent mathematical model (Wolf et al. 2007), we expect fast explorers to invest more effort into current reproduction and thus be more willing to increase parental effort than slow explorers. This is because fast explorers are thought of as having lower survival prospects and thus prioritizing current over future reproduction (Wolf et al. 2007; Nicolaus et al. 2012). Fast

explorers should thus show a higher increase in nest visit rate after the experimental brood size enlargement compared to slow explorers.

Methods

Study subjects

The data were collected from a suburban great tit population located on the Drie Eiken Campus of the University of Antwerp, Belgium (51°9'44" N, 4°24'15" E). Circa 140 nest boxes are provided for great tits to reproduce (Rivera-Gutierrez et al. 2010). Great tits can be identified using metal leg rings that they receive as nestlings (day 9/10 post-hatching) or using a unique combination of colored leg rings for adults (Rivera-Gutierrez et al. 2012). For all adults, one colored ring bears a passive integrated transponder (PIT) tag (IB Technology, Aylesbury, UK), allowing for further bird identification using antennas (Dorset Identification B.V., The Netherlands). Before the reproductive season's onset, nest boxes were regularly checked for nest building indications and then checked daily before the anticipated start of egg-laying until the last egg hatches.

Individual parents were caught at their nest box for a short period of time when feeding the chicks at day 9 post-hatching. Nestlings and unringed or untagged parents were then banded and PIT-tagged. The number of chicks present inside each nest (thereafter termed "brood size") was determined on day 9. On average, brood size in focal nests was 7.0 ± 0.3 (SE).

Assessment of exploration behavior

Exploration behavior was assessed from the 15th to the 27th of February 2013, during the winter preceding the reproductive season when the parental effort experiment was conducted. Great tits were taken out of the nest box within which they were sleeping at night. Birds were immediately brought to an experimental room following capture and placed alone in a cage ($l \times w \times h$: $0.83 \times 0.4 \times 0.5$ m) comprising a small nest box and ad libitum access to mealworms, sunflower seeds, and water. The room temperature was 5 ± 2 °C and kept under a natural light/dark cycle. On the morning following capture, birds were tested for their exploration behavior in a novel environment room ($l \times w \times h$: $4.0 \times 2.4 \times 2.3$ m) comprising five artificial trees (height \times diameter: 1.5×0.04 m) with four branches each (two at 5 cm and two at 25 cm below the top). This is a standard procedure for assessing exploration behavior in great tits (Dingemanse et al. 2002; van Overveld and Matthysen 2010; Patrick and Browning 2011; Nicolaus et al. 2012). A sliding door providing a direct access from the cage to the novel environment room was opened by the experimenter while the lights were still off inside the latter. Then,

lights were turned off in the room where the cages were held and turned on in the novel environment room, which stimulates birds to enter it. Individual behavior was then recorded for 2 min during which the number of movements between trees and between branches of the same tree was measured (thereafter referred to as “exploration score”). Birds with high exploration scores are thereafter called “fast explorers”, whereas those with low scores are called “slow explorers”. Lights from the novel environment room were turned off again, which makes the bird “freeze” and easy to catch by the experimenter. Birds were then immediately taken back to and released at the place they had been caught the day before.

Assessment of parental effort

The amount of effort into chick provisioning was assessed using parental nest visit rate (Wilkin et al. 2009; Auclair et al. 2014) following an artificial brood size enlargement (Patrick and Browning 2011). In the present study, we do not present results about the observed relationship between exploration and nest visit rate during the pre-enlargement period. A more thorough dataset using the same individuals recorded over a longer time period is the subject of a future publication elsewhere. Antennas were placed at each selected nest box in the afternoon of day 10 post-hatching. Focal nest boxes were selected on the basis that, when possible, both parents were PIT-tagged and other nest boxes from which to take chicks of the same age for the artificial enlargement were available. Overall, we used 14 nest boxes where both parents were tested for exploration behavior, four nest boxes for which only the male was exploration-tested, two nest boxes for which only the female was exploration-tested, and one nest box for which neither parent was exploration-tested. This latter nest box was obviously only used in analyses that did not involve exploration scores (i.e., between-period change in nest visit rate). Overall, 34 birds were tested for exploration behavior, whereas eight were not. However, provisioning behavior was recorded for all of them. Each setup consisted of a box (43×33×9 cm) placed on the ground close to the tree to which the nest box was attached. It contained all the electronic devices, including data logger, the battery, and the USB stick on which data about nest visits were stored. This box was linked with a thin wire to a circular antenna with cycles of ten detections per second, placed inside the nest box, and fitted with the entrance hole. The actual antenna replaced a dummy antenna that had been set before the start of the breeding season in order for birds to familiarize with it. The installation of the whole antenna system by the experimenter (MD) was not to last more than a couple of minutes, thus minimizing disturbance at the nest. The artificial brood size enlargement occurred on the morning of day 13 post-hatching, when chicks’ feeding frequency peaks in great tits (Barba et al. 2009).

On day 13 post-hatching, some nest boxes that were not used in the experiment yet and for which chicks were of the same age as those of the monitored focal nest boxes were selected. The experimenter (MD) collected two chicks from these nest boxes. They were then carried and added to a focal nest (enlargement’s starting time±SE, 9:23 am ±4 min). They remained in the focal nest box for 2:30 h, after which they were placed back in their original nest. The antenna setup was removed from the focal nest box shortly afterwards.

The brood size manipulation caused parents to temporarily fly away from the nest box. We considered the time delay to return to the nest box after the enlargement as an indication of a bird’s willingness to provide parental effort despite a potential hazard. Individuals returning faster to the nest box after the manipulation are thus thought of as being more willing to provide parental effort than individuals returning later.

Data processing

We computed a similarity index indicating to what extent both partners of a given breeding pair are similar in terms of exploration behavior following the formula:

Similarity index

$$= |\text{female exploration score} - \text{male exploration score}|$$

In our sample, similarity indices range from 3 (pairs of individuals with highly similar exploration scores) to 26 (pairs of individuals with highly dissimilar exploration scores).

Nest visit rate was computed as the number of minutes per hour that an individual was detected at the nest divided by the number of minutes within an hour (i.e., 60). This method has previously been used in studies of great tits’ provisioning behavior using the same antennas’ apparatus (Wilkin et al. 2009; Patrick and Browning 2011) and is considered to reliably reflect chicks’ feeding rate (Wilkin et al. 2009). To compute the difference in nest visit rate before versus after brood size enlargement (respectively pre- and post-enlargement period), thus controlling for between-pair initial differences in nest visit rate, we quantified nest visit rate during 2:15 h before and after the manipulation. The measurement of nest visit rate after brood size enlargement started 15 min after the manipulation to allow parents to recover from the associated disturbance (see Limbourg et al. (2013)). We chose this duration as birds were re-detected by the antenna after a median delay of 7.5 min (interquartile range, [3,14]). Eighty-eight percent of the birds (37 out of 42) were re-detected by the antenna within the 15-min period following the manipulation. Analyses conducted only with these individuals that were re-detected by the antenna within the 15-min period substantially yield the same results (not shown). For each parent, we recorded the time delay (in number of minutes) it took to come back to its nest

after the manipulation as a measure of willingness to provide parental effort. The relative change in nest visit rate following

brood size enlargement was computed for each individual as follows:

$$= \frac{\text{Relative change in nest visit rate}}{\text{Nest visit rate during the pre enlargement period}}$$

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

The computation of this index indeed allows for a control of potential initial differences in nest visit rate between pairs. Also, it enables us to reduce the number of predictors in our models, thus diminishing the risk of overloading our models with many parameters given our small sample size. The relative change in nest visit rate was log-transformed for every analysis so as to reach normality (Shapiro test $W=0.96$, $P=0.16$) and be bounded by minus and plus infinity rather than -1 and plus infinity otherwise.

Statistical analyses

Statistical models were built to, first, investigate any potential link between time delay to return to the nest after the brood size enlargement and exploration behavior; second, determine whether brood size enlargement was efficient at stimulating higher nest visit rates; third, examine whether fast explorers increased their nest visit rate more following brood size enlargement than slow explorers; and fourth, test whether the increase in nest visit rate was linked to the similarity in exploration behavior between members of a pair. In the present paper, we did not intend to test the relationship between brood size and exploration, which will be the subject of another publication elsewhere with a more thorough dataset. However, we added the variable “brood size” as a co-variate in most of our models. Models were, otherwise stated, computed using the “glmer” command from the “lme4” R package (Bates et al. 2014). We proceeded to stepwise backward deletion of the least significant term until only significant variables remained in the model with a significance threshold set at $P=0.05$. We provided Cliff’s δ (Cliff 1996; Torchiano 2014), Pearson’s (r), and Spearman’s (r_s) correlation coefficients as effect sizes with the associated sample size (Nakagawa and Cuthill 2007).

In a first generalized linear mixed model (GLMM), we set time delay (i.e., number of minutes between the manipulation and bird detection at the nest) as a response variable. Predictors were brood size and the triple interaction between sex, exploration score, and partner’s exploration score. “Pair” was added as a random intercept variable to account for the non-independence of females’ and males’ behavior within pairs. We set the model error structure to negative binomial as our response variable showed signs of overdispersion. We therefore used the “glmmADMB” R package to analyze this model (Fournier et al. 2012; Skaug et al. 2014).

In a second GLMM, we set nest visit rate as a response variable. To this end, we used the *cbind* command including both the number of minutes per hour that a given bird had been detected by the antenna and the number of minutes per hour that the bird had not been detected by the antenna (see Crawley 2007). Brood size and the interaction between period (pre- and post-enlargement) and sex were added as predictors. In order to control for the non-independence of males and females’ behavior within the same pair and for the repeated measures of the same individual across the two periods, individual ID, nested within pair, was set as a random intercept factor. We also tested this model with “period” added as a random slope factor, as recommended by Schielzeth and Forstmeier (2009). The error structure was set to binomial.

Using correlation analyses, we investigated the potential relationship between nest visit rate before brood size enlargement on day 13 and the change in nest visit rate following brood size enlargement following Tu and Gilthorpe’s (2007) standardized procedure (David et al. 2012). This is to test whether the increase in provisioning effort following brood size enlargement depends on the amount of provisioning provided beforehand. We may indeed expect individuals provisioning at a high rate to be less capable of increasing their effort following brood size enlargement.

In a third GLMM, we set the log-transformed relative change in nest visit rate (see above) as the response variable. Brood size and the interaction between exploration score, partner’s exploration score, and sex were added as predictors. To account for the non-independence of males and females’ behavior within the same pair, we added “pair” as a random intercept variable. The error structure was set to Gaussian. We could not add one’s partner relative change in nest visit rate as a predictor in this model as, due to its very random effect structure, it would have prevented it from converging properly. We have thus tested the correlation between relative change in nest visit rate and one’s partner’s aside.

In a fourth GLMM, we tested the relationship between the relative change in nest visit rate and the similarity index (see above). The log-transformed relative change in nest visit rate was defined as the response variable, and similarity index was set as a predictor. We added “pair” as a random intercept variable and set the model error structure to Gaussian.

Table 1 Results of the models testing the relationship between the time delay taken by birds to return to the nest after brood size enlargement and sex, brood size, exploration score, and partner's exploration score (significant terms are highlighted in *italic*)

	Time delay to return to the nest	
	<i>z</i>	<i>P</i>
<i>Brood size</i>	-1.98	0.047
Partner's exploration score	-1.46	0.15
<i>Sex× exploration score</i>	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

Results

Fast explorers returned quicker to the nest after the manipulation

Time delay to come back to the nest after brood size enlargement was affected by the interaction between sex and exploration score ($z=-1.96$, $P=0.050$; Table 1) (females: Spearman's $r_s(14)=-0.05$, 95 % confidence interval (CI) = (-0.73, 0.60); males: $r_s(14)=-0.67$, 95%CI = (-0.95, -0.18); Fig. 1; Table 1), and brood size (regression's slope estimate $b\pm SE=-0.22\pm 0.11$, $P=0.047$, $r_s(28)=-0.46$, 95%CI = (-0.73, -0.12); Table 1), but not by partner's exploration score ($b\pm SE=-0.03\pm 0.02$, $P=0.15$, $r_s(28)=-0.20$, 95%CI = (-0.55, 0.18); Table 1). Fast male explorers were quicker to return to the nest after the manipulation. No other interaction terms were found to be significant (Table 1). Both partners' time delay to return to the nestbox were positively correlated ($r_s(21)=0.47$, 95%CI = (0.07, 0.78), $P=0.025$).

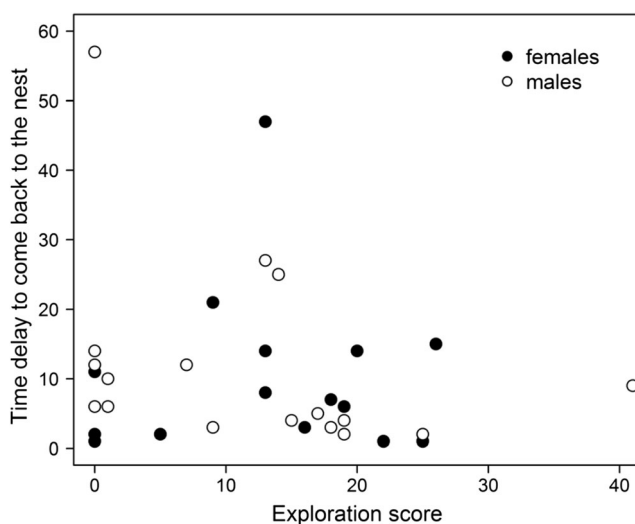


Fig. 1 Influence of exploration score on time delay to return to the nest (in number of minutes) after brood size enlargement

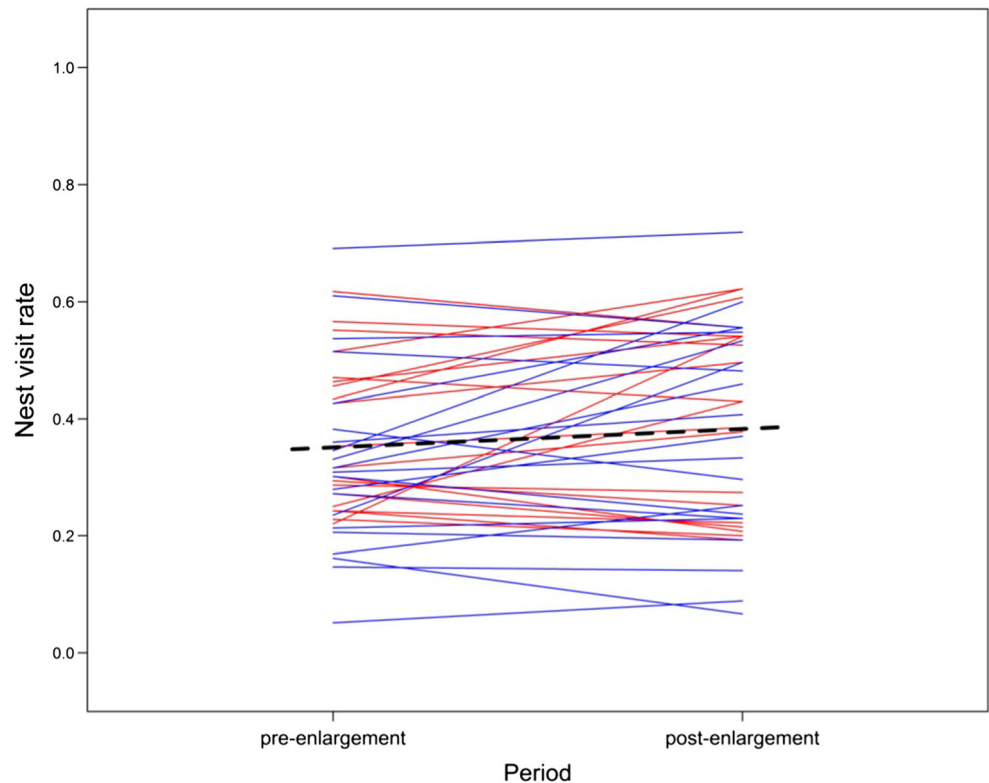
Brood size enlargement triggers higher nest visit rate

Nest visit rate significantly increased between the pre-enlargement and the post-enlargement period (pre-enlargement period: rate \pm SE=0.35 \pm 0.02; post-enlargement period: rate \pm SE=0.39 \pm 0.03; $b\pm$ SE=0.18 \pm 0.04, Cliff's $\delta=0.23$, 95%CI = (-0.14, 0.36); $\chi^2=19.85$, df=1, $P<0.0001$; Fig. 2), irrespective of sex (interaction sex \times period: $\chi^2=0.77$, df=1, $P=0.38$). However, the effect of the period no longer remained significant when "period" was added as a random slope factor in the model ($b\pm$ SE=0.15 \pm 0.09; $\chi^2=2.54$, df=1, $P=0.11$). Brood size had a significant positive effect on nest visit rate ($b\pm$ SE=0.30 \pm 0.08; $\chi^2=11.37$, df=1, $P<0.001$; $r_s(84)=0.48$, 95%CI = (0.28, 0.64)). The change in nest visit rate following brood size enlargement was not related to nest visit rate before the enlargement ($r(42)=-0.18$, 95%CI = (-0.46, 0.14), $P=0.27$; see "Methods") nor was it significantly predicted by time delay to come back to the nest after the manipulation ($r_s(42)=-0.05$, 95%CI = (-0.36, 0.27), $P=0.78$).

Partners' combined exploration scores influence parental effort

The relative change in nest visit rate was significantly affected by the interaction between sex, exploration score, and one's partner exploration score ($\chi^2=5.36$, df=1, $P=0.021$) but not by brood size ($b\pm$ SE= \pm 0.06; $\chi^2=0.86$, df=1, $P=0.35$). Taking each sex separately, the interaction between exploration score and one's partner exploration score was significant in males ($t_{10}=3.48$, $P=0.006$; Fig. 3a) but not in females ($t_{10}=1.21$, $P=0.25$; Fig. 3b). Males paired with a female of similar exploration score increased their nest visit rate more than males paired with a female of dissimilar exploration score (Fig. 3a). In females, the relative change in nest visit rate was not related to exploration score ($b\pm$ SE=0.01 \pm 0.01, $t_{11}=0.91$, $P=0.38$) nor partner's exploration score ($b\pm$ SE=0.01 \pm 0.01, $t_{12}=0.83$, $P=0.42$). However, the

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



similarity index was negatively linked to the relative change in nest visit rate in females ($b \pm SE = -0.02 \pm 0.01$, $t_{12} = -2.47$, $P = 0.030$, $r_s(14) = -0.59$, $95\%CI = (-0.80, -0.27)$; Fig. 4), as well as in males ($b \pm SE = -0.04 \pm 0.01$, $t_{12} = -2.89$, $P = 0.014$, $r_s(14) = -0.60$, $95\%CI = (-0.88, -0.10)$; Fig. 4), indicating that effort into

provisioning indeed was higher in pairs of birds with similar exploration behavior.

Individual relative change in nest visit rate was found to be positively and significantly related to one's partner's ($r(21) = 0.46$, $95\%CI = (0.04, 0.74)$, $P = 0.033$; Fig. 5).

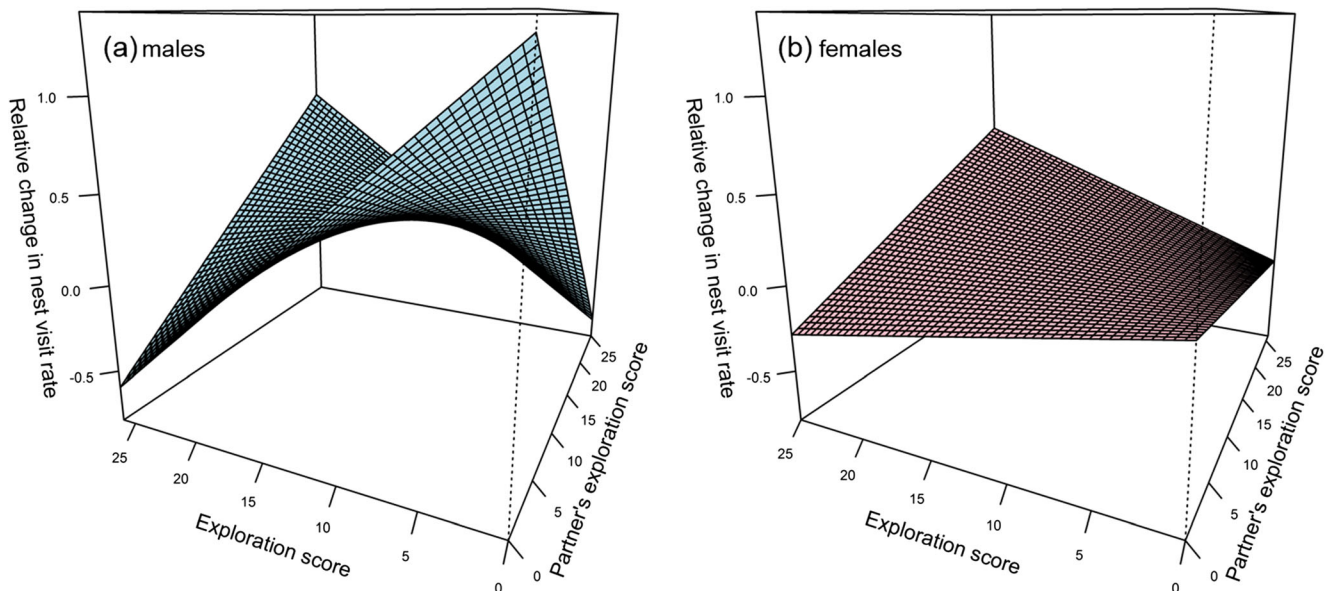
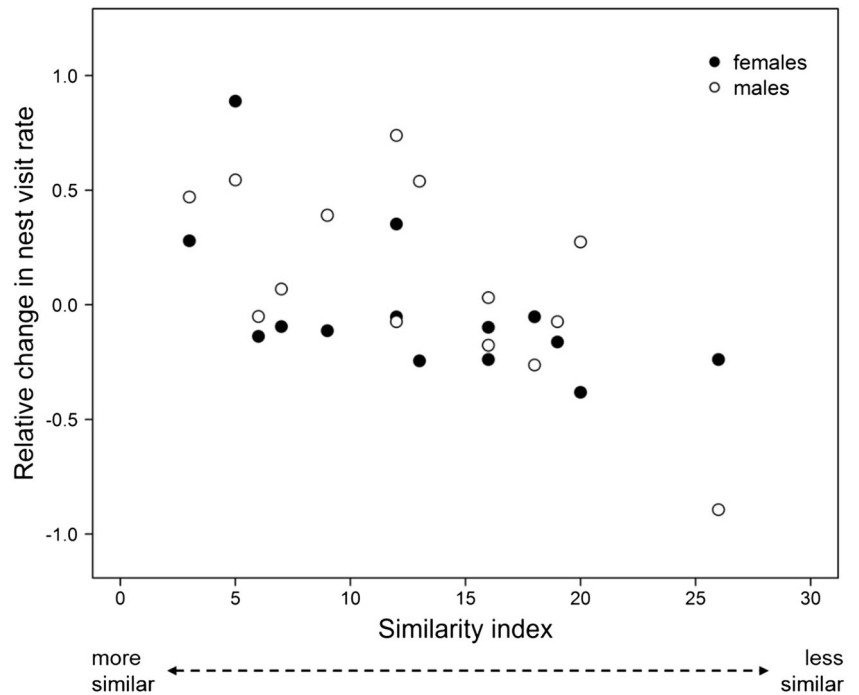


Fig. 3 Relationship between individual exploration score, partner's exploration score, and relative change in nest visit rate in males (a) and females (b). Regression planes represent the models' predictions. The relative change in nest visit rate was log-transformed (see “Methods”)

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”)



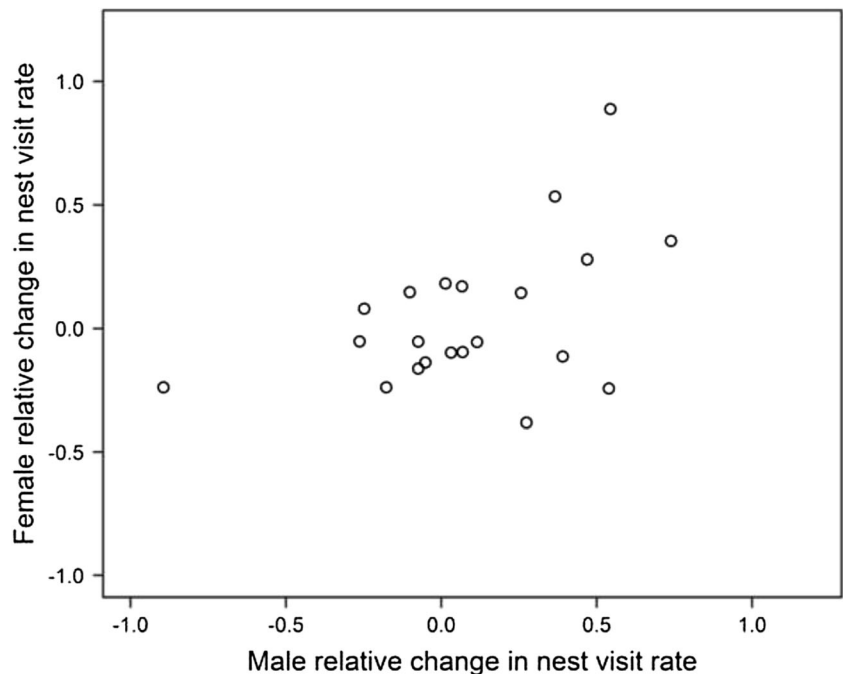
Discussion

The extended POLS hypothesis provides clear predictions about the expected relationship between within-population variation in boldness-like behaviors and life-history traits. In the present paper, we conducted a test of the relationship between exploration behavior and willingness to provide parental effort in a wild great tit population. Below we discuss the scope and limitations of

our findings and their relevance and implication in relation with theory.

The artificial enlargement of brood size was designed to stimulate individuals to put more effort into chicks provisioning than they would have normally done. Also, the computation of the relative increase in nest visit rate controlled for potential initial between-pair differences in provisioning rate, providing a “control” measure to the nest visit rate as quantified after the enlargement. Despite this control, it remains

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”)



possible that the relative increase in nest visit rate may have been influenced by any natural dynamic daily pattern of parental provisioning, something that we were not able to control in this experiment. However, if provisioning rate has been shown to peak at dawn and dusk in great tits (Patrick and Browning 2011), the daily pattern of provisioning was shown not to differ between individuals with varying exploration behaviors (Patrick and Browning 2011). We thus think that it is unlikely that the observed relationship between the relative increase in nest visit rate and exploration was the mere outcome of variation in daily patterns of provisioning. We believe that the brood size manipulation was appropriate to identify which individuals and to what extent they were willing to put more effort into parental duties and thus to place more weight onto current reproduction than others.

Nest visit rate was computed from the proportion of minutes per hour that a bird was detected by the antenna placed at the nest entrance (Patrick and Browning 2011). Although this method does not give an exact measure of how much time parents spend at the nest or any clue about the quantity and quality of food brought to the chicks, it has already been used in previous studies (Patrick and Browning 2011) and shown to reliably reflect chicks' provisioning rate (Wilkin et al. 2009). We are thus confident that our estimate of nest visit rate is a reliable proxy for parental provisioning rate and possibly for the amount of food brought to the offspring. The possibility yet remains that parents visiting more also bring lower-quality food than others. Unfortunately, this issue cannot be investigated using the present experimental procedures and would deserve further research.

The average increase in nest visit rate between the two periods was found to be rather low (4 %) and even non-significant when “period” was added as a random slope factor in the model, providing at best only little evidence that birds increased their provisioning rate after the brood size enlargement. Also, several individuals did not increase but decreased or kept their nest visit rate stable across the two periods (see Fig. 2). The possibility exists that some individuals may simply have not responded to the manipulation for several reasons: on the one hand, they may not have had sufficient time to detect and respond to the manipulation (2 h and 15 min). On the other hand, some individuals may not have responded to the enlargement because they had already reached their maximum level of effort into provisioning before the manipulation. However, we did not find any significant correlation between nest visit rate before the manipulation and the increase resulting from the manipulation, which makes the latter possibility unlikely. It may also be that some birds did not respond to the manipulation because their partner responded sufficiently (the reproductive compensation hypothesis; Gowaty et al. 2007), but we think that this also is unlikely given the positive relationship that we found between an individual's relative change in nest visit rate and its partner's

(Hunt and Simmons 2002), which on the contrary is more indicative of a social facilitation phenomenon. Further studies would be needed to understand why some birds are responsive and some are not.

The importance of the social environment when testing the POLS hypothesis

In accordance with the extended POLS hypothesis, we found that fast male explorers were quicker to come back to the nest after brood size enlargement than slow explorers, a finding reminiscent of a recent comparable result during the incubation stage in the same species (Cole and Quinn 2014). In addition, the relative change in nest visit rate was influenced by the interaction between an individual's exploration score and its partner's, at least in males. Individuals within assorted pairs for exploration scores (fast–fast explorers and slow–slow explorers) showed a higher increase in nest visit rate than individuals within non-assorted pairs, irrespective of their own exploration behavior. In females, we detected no effect of exploration behavior on the relative increase in nest visit rate. Yet, based on the correlation between the similarity index and the relative increase in nest visit rate, females paired with a male of similar exploration behavior were found to be more likely to increase their nest visit rate than in dissimilar pairs. We believe that this discrepancy may come from our small sample size and a lack of statistical power in the first mentioned linear model. We indeed acknowledge that the sample size of our study is pretty low and further studies would be needed to test the generalizability of these results. That said, our findings provide only partial support for the extended POLS hypothesis which predicts that fast explorers should, all else being equal, provide more effort into current reproduction than slow explorers. Indeed, in the present study fast explorers provisioned their brood more when paired with a fast partner than when paired with a slow one. Conversely, slow explorers provisioned their offspring less when paired with a fast explorer than when paired with a slow explorer. The importance of combined behavioral types within breeding pairs is reminiscent of previous findings that assortment for behavioral traits affects reproductive fitness in pairs of great tits (Dingemanse et al. 2004), zebra finches (*Taeniopygia guttata*) (Schuett et al. 2011), Steller's jays (*Cyanocitta stelleri*) (Gabriel and Black 2012), eastern bluebirds (*Sialia sialis*) (Harris and Siefferman 2014), and guppies (*Poecilia reticulata*) (Ariyomo and Watt 2013). The functional consequences and the reasons why it may be optimal for individuals to breed with partners of similar behavioral type remain unclear so far (Kralj-Fišer et al. 2013). Specific combinations of behavioral types within breeding pairs may affect brood provisioning efficiency (Mutzel et al. 2013), for instance, through provisioning synchronization (Mariette and Griffith 2012; see van Rooij and Griffith (2013)). The extent to which (1) pairs

of partners with similar exploration behavior are better synchronized and (2) better synchronization leads to higher reproductive success remains to be determined. The positive correlation between both partners' time delay to return to the nest and between both partners' relative change in nest visit rate, while confirming previous studies (Hinde 2006; Westneat et al. 2011), also suggests that such synchronization phenomenon could be at work in our study. Indeed it may be that social facilitation leads partners to change their nest visit rate to the same extent and that any sort of social facilitation effect is more salient when partners are of similar exploration behavior. However, this interpretation remains speculative and more work is needed to disentangle the complex interplay among partners' behavioral types, provisioning behavior, and reproductive success (Mutzel et al. 2013).

The interaction between individual exploration score and partner's exploration score in determining brood provisioning effort suggests the importance of the social environment in shaping the relationship between boldness-like behaviors and reproduction-related activities, and fitness-maximizing traits in general (Bergmüller and Taborsky 2010; Webster and Ward 2011). It is especially important as an individual's reproductive success greatly depends on its partner's investment into breeding in biparental care species. Testing for a positive relationship between boldness-like behaviors and reproductive effort may thus become inconclusive because of the social environment's influence (in the present case, one's partner's behavior). In particular, the importance of behavioral compatibility for reproductive fitness within breeding pairs (Spoon et al. 2006) may override the positive association between exploration and provisioning effort. Boldness-like behaviors are known to be substantially affected by the social environment (Mainwaring et al. 2011; Webster and Ward 2011). We believe that it would be elusive to ignore its influence (be it a constraint or a facilitator) when testing predictions of the extended POLS hypothesis in social species,

especially in a reproductive context where both partner's fitness prospects converge. Taking the social environment into account should involve studying pairing patterns with respect to boldness-like behaviors and determining the functional relationships between boldness-like traits and fitness (i.e., questioning what the factors mediating the link between both are) (Patrick and Browning 2011; Mutzel et al. 2013).

POLS hypothesis and the multidimensionality of reproductive investment

Overall, our results provide, at best, partial support for the extended POLS hypothesis with possible sex effects. Our findings differ from a previous correlational study in wild blue tits (*Cyanistes caeruleus*) that showed a positive relationship between exploration behavior and brood provisioning rate in females only (Mutzel et al. 2013). Our results also differ from another study using a similar experimental design that did not identify any significant link between exploration and brood provisioning in great tits (Patrick and Browning 2011). The possibility remains that various wild great tit populations exhibit different patterns of behavioral correlations depending on the specific selective pressures or the constraints they face or on their particular life-histories (Adriaenssens and Johnsson 2009; Patrick and Browning 2011). Finally, in western bluebirds (*Sialia mexicana*), male provisioning rate has been found to be negatively related to aggressiveness (Duckworth 2006). In this latter study, the direction of the relationship between parental effort and boldness-like traits goes against the extended POLS hypothesis' predictions. However, it is noteworthy that aggressiveness may be related to several functional behaviors that a given male may have to trade off against one another. In the case of western bluebirds, for example, more aggressive males spend more time defending their nest against potential predators and competitors (Duckworth 2006). This can reasonably be considered as

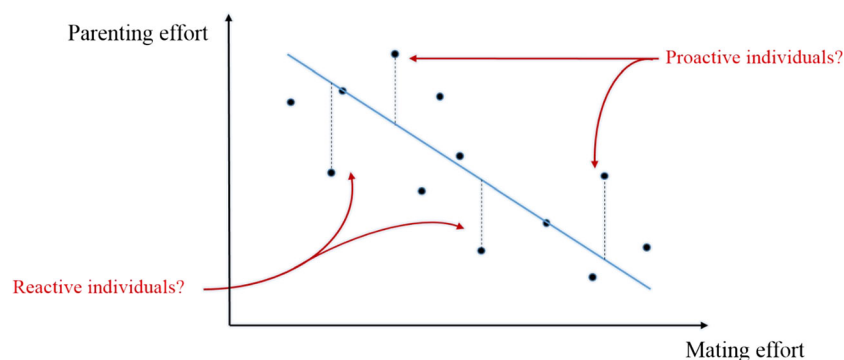


Fig. 6 Integration of various reproduction-related behaviors into a single test of the extended POLS hypothesis. Insofar as different components of reproduction can be related with one another, the overall individual effort into reproduction can be assessed by taking the residuals of the regression from the effort provided into one component on the other (principal components analyses may be considered when more than two components are

involved). According to the extended POLS hypothesis, proactive individuals should overall invest more into reproduction-related activities than reactive individuals. In this hypothetical example of a trade-off between parenting and mating effort, proactive individuals are then on average expected to have higher residual values than reactives

investment into a reproduction-related activity as a male's reproductive fitness likely depends on keeping the nest safe away from potential hazards. This is because investment into current reproduction may concern various dimensions of reproductive behavior, such as nest defense (Hollander et al. 2008), extra-pair sexual behavior (Patrick et al. 2012), or parental care (Barnett et al. 2012), that the link between boldness-like behavioral variation and brood provisioning effort may differ among populations or species. This possibility argues in favor of the necessity to confirm, generalize, and extend the present findings to other species and/or other populations of the same species. This is important in order to refine the extended POLS hypothesis, and understand unexpected associations between variables (David et al. 2011b; Adriaenssens and Johnsson 2011). Also, we encourage the simultaneous study of multiple behavioral dimensions within the same functional context (e.g., in a reproductive context: signaling, parenting, and so on...) insofar as these various dimensions may not be all maximized at the same time and may be traded off against one another (Fig. 6). These trade-offs may contribute to confound the relationships between boldness-like behaviors and reproduction-related activities expected under the extended POLS hypothesis' framework.

Conclusion

To conclude, our findings indicate that both an individual's behavioral type and its partner's can be critical in its decision to provide more or less effort into brood provisioning. This interaction is supposed to have a great impact on the relationship between boldness-like behaviors and reproduction-related activities and thus on the testing of the extended POLS hypothesis' predictions. Future studies should then carefully consider the social environment (Bergmüller and Taborsky 2010) when testing predictions of the extended POLS hypothesis. Further investigations are also needed to integrate various reproduction-related activities together into a single test of the extended POLS hypothesis.

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Ethical standards This study was approved by the ethical committee of the University of Antwerp (ID number 2011-31), and it was performed in accordance with Belgian and Flemish laws. The Belgian Royal Institute for Natural Sciences (Koninklijk Belgisch Instituut voor Natuurwetenschappen) provided ringing licences for authors and technical personnel.

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