

# An offspring signal of quality affects the timing of future parental reproduction

Flore Mas\* and Mathias Kölliker

Zoological Institute, Evolutionary Biology, University of Basel, Vesalgasse 1, 4051 Basel, Switzerland

\*Author for correspondence (floremas@hotmail.com).

**Solicitation signals by offspring are well known to influence parental behaviour, and it is commonly assumed that this behavioural effect translates into an effect on residual reproduction of parents. However, this equivalence assumption concerning behavioural and reproductive effects caused by offspring signals remains largely untested. Here, we tested the effect of a chemical offspring signal of quality on the relative timing and amount of future reproduction in the European earwig (*Forficula auricularia*). We manipulated the nutritional condition of earwig nymphs and exposed females to their extract, or to solvent as a control. There were no significant main effects of exposure treatment on 2nd clutch production, but exposure to extracts of well-fed nymphs induced predictable timing of the 2nd relative to the 1st clutch. This result demonstrates for the first time that an offspring signal *per se*, in the absence of any maternal behaviour, affects maternal reproductive timing, possibly through an effect on maternal reproductive physiology.**

**Keywords:** parent–offspring conflict; offspring begging; chemical communication; *Forficula auricularia*; parental care

## 1. INTRODUCTION

It is well known that solicitation signals by offspring influence parental behaviour and are condition-dependent [1], which is consistent with predictions of models for the evolution of parent–offspring interactions [2–6]. A core assumption of all these models is that offspring signals not only affect the behaviour of parents, but that they can also affect their residual fecundity. The well-documented purely behavioural effects on parents may be transient and merely reflect short-term behavioural dynamics [7,8]. Only if offspring signals have the potential to affect residual parental reproduction can selection favour exaggeration and manipulative potential (as under conflict: [6]), and/or the co-adaptation with parental sensitivities [5]. Evidence for such an effect comes from a recent cross-fostering experiment in the canary (*Serinus canaria*) showing a negative correlation between the solicitation of foreign nestlings and the subsequent clutch size produced by foster females [9].

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.1094> or via <http://rsbl.royalsocietypublishing.org>.

Received 18 November 2010  
Accepted 8 December 2010

Theory more specifically assumes that the fitness effects of offspring signals on parents are equivalent to (or a direct function of) the behavioural effects (see [10] for discussion of ‘investment ESS’ versus ‘food ESS’), that is, offspring signals should have no effect on parental residual reproduction in the absence of expressed care behaviour. This equivalence assumption has to our knowledge not been previously tested and may not apply if offspring signals evolved direct influences on maternal reproductive physiology (i.e. ‘primer effect’; [8,11]). The potential for direct offspring influences on maternal reproduction is of evolutionary interest, because it modifies selection on offspring and parental behaviours. A hypothetical offspring signal that suppresses future reproduction by parents would eliminate any evolutionary cost of parental resource provisioning in terms of residual reproduction, disrupting the link between provisioning and investment [8]. Direct testing of this assumption requires manipulation of offspring signals independent of other traits, and measurement of effects on parents without the expression of care behaviours, both of which were difficult in the past.

Here, we provide such an experimental test in the European earwig (*Forficula auricularia*). We tested the direct effect of a previously described offspring signal of quality [12] on maternal residual fecundity in the absence of expressed maternal care. Female earwigs produce one or two clutches in their lifetime [13], provide maternal care for few weeks after hatching and adjust maternal behaviour to a condition-dependent mix of cuticular hydrocarbons (CHC) produced by the nymphs on their cuticle [12,14]. This system allowed us to experimentally expose females to the isolated offspring signal in the absence of expressed maternal behaviour.

## 2. MATERIAL AND METHODS

Adult earwigs were collected in Dolcedo (IT) in July 2009 and kept in the laboratory in mixed-sex groups of 30 males and females with ad libitum food [15]. Upon egg laying, the date and size of 1st clutches were noted and the eggs with their tending mothers placed at 15°C in complete darkness. At hatching, the date and number of hatched nymphs were recorded and families were placed at 14 L : 10 D and a constant temperature of 20°C. Females and 15 of their one-day-old nymphs were transferred for four days to new Petri dishes (10 × 2 cm) with humid sand as substrate and ad libitum food. On day 5, females were separated from their nymphs and set-up in new Petri dishes containing a small exposure chamber [12]. Females were then randomly assigned to an exposure treatment. They were exposed either to extract from high-food (HF) brood ( $n = 42$ ), extract from low-food (LF) brood ( $n = 42$ ) or pure solvent as control (C) ( $n = 43$ ) during nine days. Extracts were obtained following the methods by Mas *et al.* [12] based on groups of usually 35 nymphs in experimentally manipulated nutritional condition. For each female, an extract from an independent group of nymphs was used (see the electronic supplementary material for more details).

On day 14, the females were transferred to a new Petri dish and provided with food twice a week until 2nd clutch egg-laying. The laying date and size for 2nd clutches, their hatching date and offspring numbers were recorded. For consistency, we included only those 2nd clutches that were laid within 60 days after hatching of the 1st clutch (representing extreme values; [15]). Note that inclusion of the nine later 2nd clutches did not qualitatively alter our results.

Our laboratory population is maintained under an artificial seasonality including ‘winter’, ‘spring/summer’ and ‘autumn’, simulated by photoperiod and temperature differences [15]. Thus, we could record temporal patterns of oviposition with regard to this seasonality as measures of the timing of breeding under laboratory conditions.

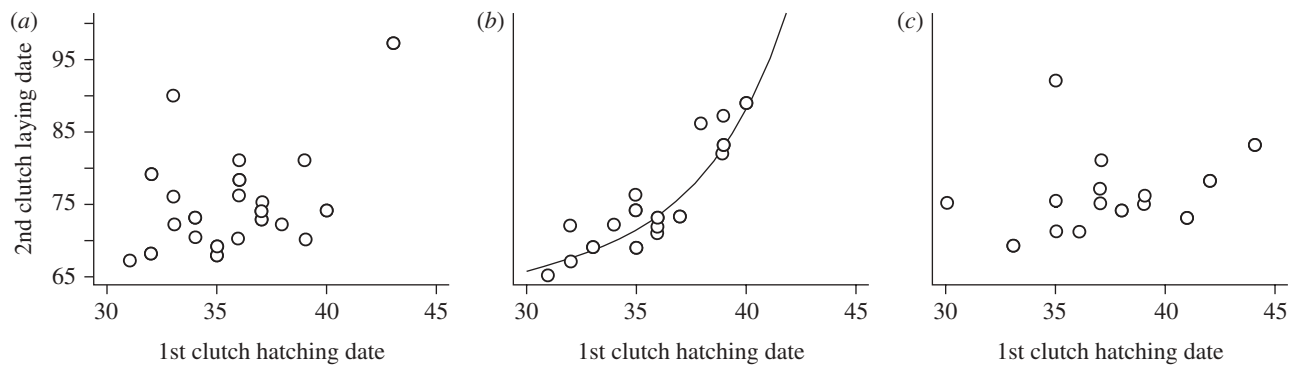


Figure 1. Relationship between 2nd clutch laying date and 1st clutch hatching date after exposure to (a) solvent (control females 'C'); (b) extract from high-food nymphs (HF exposure treatment); and (c) extract from low-food nymphs (LF exposure treatment). In (b) the solid line corresponds to the fit from our model (back-transformed model prediction:  $r^2 = 0.78$ ;  $p < 0.001$ ). Day 0 on the axes refers to 12 November 2009.

Statistical analysis was performed using R statistics software v. 2.11.1 (<http://www.r-project.org>) and JMP v. 8.0.2 [16]. The effect of exposure treatment on female reproductive parameters (frequency, timing and size of 2nd clutches/broods) was tested using logistic regression (LR) and analysis of covariance (ANCOVA) models, respectively. For each model, we included the exposure treatment as fixed factor, and the 1st clutch parameter corresponding to the analysed 2nd clutch parameter as covariate, and the interaction between treatment and the covariate. Female pronotum area (i.e. a measure of structural size) was never significant and removed from the models. When the residuals of a model were not normally distributed, a Johnson Su transformation [17] was applied.

### 3. RESULTS

From the 127 tested females, 56 laid a second clutch within 60 days of hatching of the 1st clutch. There were no significant main effects of exposure treatment on the frequency (LR- $\chi^2 = 1.51$ ,  $p = 0.47$ ), the size (number of eggs:  $F_{2,50} = 2.13$ ,  $p = 0.12$ ; number of hatchlings:  $F_{2,50} = 1.79$ ,  $p = 0.17$ ) or the timing (egg laying date:  $F_{2,50} = 0.04$ ;  $p = 0.96$ , hatching date:  $F_{2,49} = 0.03$ ,  $p = 0.97$ ) of the 2nd clutch (see the electronic supplementary material, table 1 for summary of life-history data according to treatment).

However, the exposure treatment significantly affected the relative timing of 2nd clutch production through an interaction with hatching date of the 1st clutch (interaction exposure treatment  $\times$  1st clutch hatching date:  $F_{2,50} = 6.35$ ,  $p = 0.003$ ; figure 1). This effect was due to a strong positive, and statistically significant, relationship between the dates for 2nd and 1st clutch production in females exposed to extracts from HF broods (slope ( $\pm$ s.e.): 0.39 ( $\pm 0.05$ );  $r^2 = 0.78$ ;  $F_{1,17} = 57.82$ ,  $p < 0.001$ ; figure 1b) and lack thereof in females exposed to solvent only (C; slope ( $\pm$ s.e.): 0.14 ( $\pm 0.07$ );  $r^2 = 0.16$ ;  $F_{1,21} = 3.96$ ,  $p = 0.06$ ; figure 1a) or extracts from LF brood (slope ( $\pm$ s.e.): 0.06 ( $\pm 0.05$ );  $r^2 = 0.09$ ;  $F_{1,15} = 1.51$ ,  $p = 0.24$ ; figure 1c).

### 4. DISCUSSION

Our study demonstrated that the condition-dependent cuticular extracts of earwig nymphs *per se*, and in the absence of other offspring traits or maternal behaviour, differentially affect the relative timing of future reproduction of their mothers. The nature of effect was more complex than anticipated: there were no

significant main effects of exposure treatment on the frequency, size or timing of 2nd clutch production. Rather, the extracts of high-condition (HF) nymphs induced highly predictable maternal timing of 2nd clutch relative to the 1st clutch. In this treatment, early females consistently laid their 2nd clutch soon after the first hatched, whereas late females delayed their 2nd clutch substantially. Conversely, females exposed to solvent (C) or extract of low-condition (LF) nymphs showed no significant predictability in the relative timing of 2nd clutches.

This pattern may be explained by a hypothetical scenario of co-adaptation [5] between the chemical offspring signal of quality and seasonal variation in the reproductive value of maternal behaviour for nymphs in 1st versus 2nd clutches. Early in the season, earwig nymphs experience less dense populations, less competition and risk of cannibalism and more time for development and mating before winter [13,18]. For 1st clutch nymphs in good nutritional condition survival may, under these circumstances, be sufficiently high even with shorter maternal care. But late in the season, longer maternal care for these high condition nymphs may be particularly valuable to further enhance their survival prospects. Hence, it may pay females with late 1st clutches to care for longer and delay the 2nd clutch. This relationship may be less or absent if offspring are in poor condition (our LF treatment) or in the absence of information on offspring condition (our control group C). A comparable, albeit purely behavioural, seasonal effect of an offspring signal of quality on parental food allocation was found in Alpine swifts (*Apus melba*) and starlings (*Sturnus vulgaris*) [19]. When offspring UV reflectance was manipulated, early breeding parents preferentially fed offspring with experimentally reduced UV reflectance, while late breeding parents favoured to feed control offspring with full UV reflectance. Whether in earwigs the apparent seasonal variation in the effect of nymph CHC on the timing of 2nd clutch production in *F. auricularia* reflects variation between early and late females in their responsiveness to a fixed chemical signal of quality, seasonal variation in the signal of quality emitted by nymphs of early versus late clutches, or both will have to be investigated in the future.

We previously showed that the main effects of earwig chemical signal of quality is on maternal behaviours such as provisioning [12], grooming and aggression [14], and that maternal behaviour (i.e. exposure to and interaction with nymphs) has a main delaying effect on the timing of 2nd clutches [15]. The present study demonstrates that offspring signals can have a direct influence on maternal reproductive physiology (i.e. through a primer effect; [8,11]), which differs from the behavioural effects. Primer effects of offspring signals on caregivers have only rarely been studied. The only other example for such effects that we are aware of is the brood pheromone in bees (*Apis mellifera*) which alters the timing of developmental transition from the nurse to the forager stage in workers [20,21].

This study shows that the equivalence assumption of behavioural and reproductive effects of offspring signals on parents does not necessarily hold. By affecting parameters of future reproduction of mothers directly, rather than indirectly through resource provisioning, the offspring signal shortcuts the link between the signal, care provisioning and the evolutionary cost of parental behaviour. Such an offspring signal may alter the selection operating on care provisioning, which in turn may have important consequences for the evolution of family interactions.

We thank Joël Meunier, Matt Hall and two anonymous referees for very valuable comments. This study was financed by the Swiss National Science Foundation (grant no. PP00P3\_119190 to M.K.) and the Emilia-Guggenheim Stiftung (PhD support to F.M.).

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