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When earwig mothers do not care to share: parent-offspring competition and the evolution of family life

Running title: Parent-offspring competition and family life

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SUMMARY

1. Kin competition often reduces – and sometimes entirely negates – the benefits of cooperation among family members. Surprisingly, the impact of kin competition on the fitness effects of family life only received close scrutiny in studies on sibling rivalry, whereas the possibility of parent-offspring competition has attracted much less attention. As a consequence, it remains unclear whether and how parent-offspring competition could have affected the early evolution of parental care and family life.
2. Here, we examined the occurrence and consequences of parent-offspring competition over food access in the European earwig *Forficula auricularia*, an insect with facultative family life reminiscent of an ancestral state. Specifically, we (i) raised earwig offspring under food limitation either together with or without their mother, and (ii) tested whether and how the – potentially competitive – weight gains of mothers and offspring during family life affected the offsprings' survival rate and morphology, and the future reproductive investment of their mother.
3. In line with the occurrence of local parent-offspring competition over food access, we showed that high maternal weight gains during family life reduced the survival prospects of maternally tended offspring, while they increased the mothers' investment into the production of a second clutch (but not the body size of the surviving offspring). Conversely, high offspring weight gains generally increased the offsprings' survival, but did so to a larger extent when they were together with their mother. Intriguingly, mothers that had exhibited a low initial weight showed especially high weight gains.

4. Overall, our results demonstrate that maternal presence under food restriction triggered a local competition between mothers and their offspring. This competition limited offspring survival, but allowed mothers to increase their investment into future reproduction and/or to maintain their current body condition. On a general level, our findings reveal that parent-offspring competition can counteract the benefits of (facultative) parental care, and may thus impede the evolution of family life in resource-poor environments.

Keywords: European earwig; environmental conditions; family life; kin competition; orphaning; parental care; parent-offspring competition; parent-offspring conflict.

INTRODUCTION

The association of offspring with their parents after birth or hatching (defined as family life; Mock & Parker 1997) is a rare, but taxonomically widespread phenomenon (Royle, Smiseth & Kölliker 2012) that can only evolve if the fitness benefits of family interactions outweigh the costs of a prolonged association of the family members (Alonso-Alvarez & Velando 2012). The fitness benefits of family life predominantly derive from the expression of parental care (Costa 2006; Wong, Meunier & Kölliker 2013), which ultimately increases the survival and/or quality of tended juveniles (Klug, Alonso & Bonsall 2012). By contrast, the costs of family life typically result from kin competition among family members for limited resources and reproduction (Krause & Ruxton 2002; West, Pen & Griffin 2002). This competition is known to affect crucial life-history traits such as sex allocation (Frank 1985) and aggressive behavior (West *et al.* 2001), and commonly arises during family life where juveniles strive to monopolize limited parental resources (sibling rivalry; Mock & Parker 1997; Roulin & Dreiss 2012). However, kin competition during family life can also arise between offspring and their parents. Such parent-offspring competition can, for instance, promote the dispersal of offspring that reached nutritional independence (Cockburn 1998; Cote, Clobert & Fitze 2007), and therefore hampers the evolution of complex family systems in cooperative breeders (Sorato, Griffith & Russell 2016). Shedding light upon the parties engaged in competition is hence crucial to advance our understanding of the cost-benefit ratio of family life, and more generally its emergence and maintenance in nature (Klug & Bonsall 2010; Klug *et al.* 2012).

The emergence of family life marks the appearance of facultative forms of (post-hatching) parental care (Smiseth, Darwell & Moore 2003; Kölliker 2007). Somewhat surprisingly, the possibility of local parent-offspring competition in species featuring such

facultative care has been poorly explored, and its impact on the early evolution of parental care and family life therefore remains unknown. This oversight conceivably results from a historical bias towards studying parental care in altricial – i.e. obligatory-caring – species (Clutton-Brock 1991), in which the scope for parent-offspring competition during early family life is limited by the low foraging capabilities of juveniles. During earlier stages of the evolution of family life (and in contemporary precocial species), however, juveniles are not fully dependent on parental resources (Smiseth *et al.* 2003; Kölliker 2007), and the early onset of offspring foraging might put them into competition with their caring parents early on. In such situations, the costs of parent-offspring competition could diminish the benefits of parental care, and might ultimately render parental presence (Scott & Gladstein 1993; Boncoraglio & Kilner 2012) and family life maladaptive altogether (Meunier & Kölliker 2012).

The intensity of competition typically depends on the environmentally determined availability of limited resources. Harsh environments could therefore have a profound impact on parent-offspring competition and the evolution of family life (Wilson 1975; Klug *et al.* 2012). The nature of this impact, however, remains controversial. On the one hand, harsh conditions should favor the evolution of family life, because the benefits of parental care are then likely substantial (Wilson 1975; Clutton-Brock 1991). On the other hand, harsh environments are expected to exacerbate the costs of care (such as an increased energy loss; Alonso-Alvarez & Velando 2012), and the limited resource availability may not only favor the deferral of parental investment (Clutton-Brock 1991; Klug & Bonsall 2007), but also increase parent-offspring competition and thus hamper the evolution of family life. In line with this hypothesis, the prolonged presence of fathers has been shown to reduce offspring survival under food limitation in *Nicrophorus vespilloides* Herbst, a burying beetle with biparental care

in which both parents feed on the carcass employed for breeding (Scott & Gladstein 1993; Boncoraglio & Kilner 2012). Moreover, food restriction has been shown to offset the benefits of maternal care in the European earwig *Forficula auricularia* L. (Meunier & Kölliker 2012), suggesting that kin competition between offspring and their tending mother might have rendered maternal presence and hence family life detrimental to offspring survival.

In this study, we investigated the occurrence and consequences of mother-offspring competition under harsh conditions (emulated by food restriction) in the European earwig *F. auricularia*. In this precocial insect, mothers provide extensive forms of care to their mobile offspring (called nymphs) for several weeks after hatching (Lamb 1976a). Maternal care includes the protection and grooming of nymphs, as well as their provisioning with food (e.g. through regurgitation; Lamb 1976b; Staerke & Kölliker 2008), and is even expressed by mothers in a bad nutritional condition (Kramer & Meunier 2016). However, post-hatching maternal presence and care are not obligatory for offspring survival (Kölliker 2007; Kölliker & Vancassel 2007), as nymphs can forage independently soon after hatching (relying on the same food resources than their mother; Lamb 1976b) and may even obtain food from their siblings (Falk *et al.* 2014; Kramer, Thesing & Meunier 2015). Consequently, the cost-benefit ratio of maternal presence in *F. auricularia* generally depends on the environmental conditions experienced by mothers and nymphs during family life (Kölliker 2007; Meunier & Kölliker 2012; Thesing *et al.* 2015).

To assess the occurrence of mother-offspring competition, we raised nymphs under food restriction either together with or without their mother, and investigated whether offspring survival was reduced when mothers consumed food and thus restricted offspring feeding (or *vice versa*). We then examined whether the condition of mothers and/or their

nymphs at hatching determined the intensity of the putative competition, as well as whether this intensity affected the mothers' future reproduction and the morphology of their (surviving) first-brood offspring. If mother-offspring competition occurred, we would expect that maternal weight gains during family life negatively affect offspring survival under maternal presence (but not absence). Moreover, we predicted that mothers exhibiting a low initial weight would compete more intensely – and thus curtail their offspring's survival more extensively - than mothers exhibiting a high initial weight. Similarly, we expected that groups of nymphs with low initial weight would compete more intensely with their mother to ensure their own survival. Finally, we predicted that intense competition might benefit mothers and the surviving offspring, for instance by enabling them to increase their investment into future reproduction and their final body size, respectively.

MATERIALS AND METHODS

Laboratory rearing and experimental design

We investigated the occurrence and potential repercussions of mother-offspring competition under harsh conditions in 128 female earwigs and their first brood. The females had been collected in July and August 2013 in Mainz, Germany and were reared under standard laboratory conditions (adapted from Meunier *et al.* 2012; see Appendix S1 in Supporting Information) until they produced their first clutch. On the first day after egg hatching, we haphazardly distributed a random subset of 32 nymphs (original brood size: 49.6 ± 1.1 nymphs; mean \pm se) among two equally sized groups. We manipulated the potential for mother-offspring competition over food access by raising one of these groups together with their mother (maternal presence-, or *MP-group*) and the other group without their mother (maternal absence-, or *MA-group*). After 16 days, mothers were removed from the MP-groups

to mimic natural family disruption (Meunier *et al.* 2012) and to determine their investment into the production of a second (and final) clutch. In parallel, the MP- and MA-nymphs were maintained in their groups, and their survival and morphology were measured upon adult emergence. Note that we excluded 16 of the 128 initially employed families from our analyses because the mother died during family life.

Harsh environmental conditions were emulated according to an established protocol (Meunier & Kölliker 2012) by providing MP- and MA-groups with a restricted amount of an artificial diet (composition detailed in Kramer *et al.* 2015) every six days for the duration of three days, respectively. This six-day cycle was initiated on the first day after hatching and repeated until the juveniles reached adulthood. The amount of food the groups received at a time was increased stepwise from 60 mg (until the end of family life) to 120 mg (until day 31) and finally to 240 mg (until adulthood; cf. Meunier & Kölliker 2012). This feeding regime successfully established scope for mother-offspring competition, as the food provided during family life was more often fully consumed before removal in MP- than in MA-groups (in 81 vs. 25 % of cases; paired Wilcoxon signed rank test: $V = 4656$, $P > 0.0001$). We also manipulated the conditions experienced by mothers after family life to investigate the effect of food availability during that period on their investment into a second clutch. To this end, isolated mothers either received 60 mg of food in a continuation of the above detailed six-day cycle (low food-treatment; $n = 54$ mothers), or an *ad libitum* amount that was renewed twice per week (high food-treatment; $n = 58$ mothers). Isolated mothers and all groups of young nymphs were kept in medium Petri dishes ($\varnothing = 9$ cm) throughout the experiment. On day 31, groups of older nymphs were transferred into large Petri dishes ($\varnothing = 14$ cm). All Petri dishes contained humid sand as substrate and a plastic tube as shelter.

Measurements

We determined the occurrence and intensity of mother-offspring competition by testing for the occurrence and strength of a negative association between maternal food consumption and offspring fitness. To this end, we measured the relative weight gains of mothers and nymphs during family life (as a proxy of food intake), and gathered the survival rate of nymphs at the end of family life and upon adult emergence in all remaining 112 families (see above). The weights of mothers were determined by weighing each mother on the first day after egg hatching and at the end of family life. Similarly, the average weights of nymphs were determined by weighing all nymphs of a family on the first day after hatching, as well as all surviving nymphs of a group at the end of family life, and then dividing these weights by the corresponding number of weighed nymphs. The *relative* weight changes were calculated by subtracting the weight at the beginning of family life from the corresponding weight at its end, and then dividing this difference by the initial weight. All mothers and nymphs were weighed to the nearest 0.01 mg using a microscale (MYA5, PESCALE, Bisingen, Germany). Offspring survival rates at the end of family life were determined by counting the nymphs that survived until day 16, and then dividing this number by the number of nymphs initially distributed to that group. Likewise, the survival rates upon adult emergence were determined by counting the nymphs that survived until adulthood, and then dividing this number by the number of nymphs alive at the end of family life. Note that two nymphs per group were removed six days after hatching to conduct an independent experiment (data not shown). These nymphs were not considered in the calculation of survival rates.

We also determined the consequences of the suspected mother-offspring competition for the future (and final) reproductive effort of mothers, as well as for the morphology of the

surviving, adult offspring. To this end, we checked all 112 isolated mothers daily for oviposition over a period of 100 days, and assessed (1) the occurrence of egg deposition and - where applicable - (2) the length of the inter-clutch interval and (3) clutch size (the number of eggs produced within three days after the onset of egg-deposition; Meunier & Kölliker 2013). The inter-clutch interval was defined as the number of days between isolation from the first brood and the deposition of the second clutch (Kölliker 2007). The morphology of adult offspring was assessed by measuring two fitness-relevant morphological traits – eye distance (a proxy of body size) and forceps length (Radesäter & Halldórsdóttir 1993) – in the first male and female adult that emerged in each group. Overall, we measured 192 males and 198 females [at least one male emerged in 92 (100), and at least one female in 94 (104) of the 112 MP- (MA-) groups]. All morphological measurements were taken under CO₂-anesthetization to the nearest 0.001 cm using a camera coupled to a stereo microscope (DFC425, Leica Microsystems Ltd, Heerbrugg, Switzerland) and operated with the software *Leica Application Suite 4.5.0*.

Statistical analyses

Establishing the occurrence of mother-offspring competition over food access requires to demonstrate that offspring fitness under maternal presence is reduced (and maternal fitness increased) when mothers restrict offspring feeding through their own food consumption (or vice versa). Accordingly, we predicted that high maternal weight gains would (1) only impair the survival and/or morphology of offspring raised under maternal presence, and (2) increase maternal investment into the production of a second clutch. To verify our first prediction, we used a generalized linear mixed model (GLMM) with binomial error distribution to test whether offspring survival rate (entered as odds ratio) was affected by offspring and maternal weight gains, maternal presence (MP or MA), and the observation period (from the beginning

until the end of family life or from the end of family life until adult emergence). An observation-level variable and Family-ID were entered into the model as random effects to account for overdispersion (Harrison 2015) and the common origin of nymphs in the MP- and MA-groups, respectively. Because a four-way-interaction between all explanatory variables shaped offspring survival (Table S1; Wald $\chi_1^2 = 7.80$, $P = 0.0052$), we split the data set by the observation period and fitted two GLMMs with the same set of variables (except the observation period) within each subset. Similarly, we fitted two separate linear mixed models (LMMs) using Family-ID as a random effect to test whether either the eye distance or the forceps length (corrected for eye distance; details in Appendix S2) of adult offspring was affected by maternal and offspring weight gains, maternal presence, and adult sex.

To examine our second prediction, we tested in two generalized linear models (GLMs) fitted with a binomial error distribution (corrected for overdispersion) and one linear model (LM) whether the weight gains of mothers and/or offspring affected the mothers' future reproduction. Each of these models included maternal and offspring weight gains, as well as the availability of food after family life (HF or LF) as explanatory variables. The GLMs were fitted using either the occurrence of 2nd clutch production or the relative investment of mothers into the production of their 2nd clutch (entered as odds ratio of 2nd to 1st clutch eggs) as a response variable. Conversely, the LM was fitted using the length of the inter-clutch interval as response variable. Note that this LM and the GLM analyzing the relative investment of mothers into their 2nd clutch were fitted on the subset of those mothers that eventually produced a second clutch. In the final step of our analysis, we investigated the determinants of maternal and offspring weight gains. To this end, we fitted one LM and one LMM that each used the weight of the mother and of the nymphs at hatching (corrected for the initial weight

of the mother; details in Appendix S3) as explanatory variables. The LM and LMM were fitted using maternal weight gain and offspring weight gain as response variable, respectively. Because this latter model was fitted on both MP- and MA-groups, we included Family-ID as a random effect.

All statistical analyses were performed with the statistics software R version 3.0.3 (<http://www.r-project.org/>). Mixed model analyses were implemented using the packages *lme4*, *car*, and *lmerTest*. Note that we scaled the 'relative weight gain of mothers' and the 'average relative weight gain of the offspring' to unit variance to avoid model bias due to collinearity between these variables (variance inflation factor < 4.0 after scaling in all models). All statistical models initially included all possible interactions between the tested variables and were then simplified via the stepwise deletion of non-significant interactions (all $p < 0.05$). Interactions between continuous variables were plotted using the package 'effects' to display the predicted relationship between the response variable and one explanatory variable for different values of the interacting variable(s) (details in Fox 2003).

RESULTS

Two independent interactions between maternal presence and, respectively, the relative weight gains of mothers and the relative weight gains of the offspring determined offspring survival until adulthood (Table 1a). In line with the occurrence of mother-offspring competition, the first interaction revealed that high maternal weight gains reduced the long-term survival of offspring when the mother was present (Fig.1a; estimate \pm se = -0.175 ± 0.070 , $z = -2.518$, $P = 0.0118$), but not when she was absent during family life (Fig.1a; estimate \pm se = 0.047 ± 0.067 , $z = 0.698$, $P = 0.4854$). Conversely, the second interaction showed that the

offspring's long-term survival increased more steeply with their weight gains under maternal presence (Fig.1b; maternal presence: estimate \pm se = 0.359 ± 0.072 , $z = 4.983$, $P < 0.0001$; maternal absence : estimate \pm se = 0.161 ± 0.067 , $z = 2.396$, $P = 0.0166$).

Offspring survival until the end of family life was shaped by a triple-interaction between maternal presence and the weight gains of mothers and their offspring (Table 1b). In particular, high maternal weight gains reduced the positive impact of high offspring weight gains on offspring survival under maternal presence (Fig.2; maternal weight gain: $\chi_1^2 = 1.083$, $P = 0.2981$; offspring weight gain: $\chi_1^2 = 0.083$, $P = 0.7736$; interaction: $\chi_1^2 = 8.278$, $P = 0.0040$). By contrast, offspring survival during family life was independent of both maternal and offspring weight gains under maternal absence (interaction: $\chi_1^2 = 2.588$, $P = 0.1077$; maternal weight gain: $\chi_1^2 = 0.276$, $P = 0.5995$; offspring weight gain: $\chi_1^2 = 0.592$, $P = 0.4416$).

The weight gains of mothers and their offspring during family life overall decreased with their own initial weight (weight gain of mother : Fig.3a, estimate \pm se = -7.202 ± 1.081 , $t = -6.663$, $P < 0.0001$; weight gain of offspring : Fig.3b, estimate \pm se = -0.091 ± 0.022 , $t_{112.00} = -4.164$, $P < 0.0001$), but were independent of each other's initial weight (weight gain of mother : estimate \pm se: -62.058 ± 48.345 , $t = -1.284$, $P = 0.2020$; weight gain of offspring : estimate \pm se: 1.685 ± 3.157 , $t_{112.00} = 0.534$, $P = 0.5940$), respectively. Notably, offspring collectively gained less weight under maternal presence (mean \pm se: 0.86 ± 0.03) than under maternal absence (0.99 ± 0.03 ; $\chi_1^2 = 23.478$, $P < 0.0001$).

Overall, 61 of the 112 mothers (54.5 %) produced a second clutch. Both the likelihood of 2nd clutch production (Table 2a) and the length of the inter-clutch interval (Table 2b) were shaped by an interaction between maternal and offspring weight gains during 1st brood family life. Intriguingly, these interactions indicated that high maternal weight gains increased the

likelihood of 2nd clutch production (Fig.4a) and decreased the length of the inter-clutch interval (Fig.4b) only if the 1st brood offspring had featured high weight gains. By contrast, high maternal weight gains actually reduced the likelihood of 2nd clutch production (Figure 4a), and increased the inter-clutch interval (Fig.4b), if they occurred in combination with low offspring weight gains. Note that the interactive effect of maternal and offspring weight gains on the length of the inter-clutch interval was contingent upon the mothers' access to food after family life, as the interaction only emerged when food was restricted (interaction: $F_1 = 6.03$, $P = 0.0234$; maternal weight gain: $F_1 = 0.11$, $P = 0.7458$; offspring weight gain: $F_1 = 0.01$, $P = 0.9364$), but not when it was provided *ad libitum* (interaction: $F_1 = 2.68$, $P = 0.1112$; maternal weight gain: $F_1 = 0.18$, $P = 0.6742$; offspring weight gain: $F_1 = 0.12$, $P = 0.7325$). Finally, the investment into 2nd clutch production increased with maternal weight gains during 1st brood family life (Table 2c; estimate \pm se: 0.228 ± 0.098 , $t = 2.322$, $P = 0.0238$), and was overall higher when mothers had received food *ad libitum* after family life (Table 2c). By contrast, the weight gains of 1st brood offspring did not affect the relative investment of mothers into their 2nd clutch (Table 2c; estimate \pm se: -0.150 ± 0.104 , $t = -1.453$, $P = 0.1516$).

Maternal presence affected the eye distance, but not the corrected forceps length, of those offspring that survived until adulthood. In particular, the eye distance of adult offspring was overall smaller when they grew up together with (mean \pm SE = 1.340 ± 0.005 mm) rather than without their mother (1.354 ± 0.005 mm; Table 3a), and overall larger in females (1.370 ± 0.005 mm) than in males (1.324 ± 0.004 mm; Table 3a). Moreover, eye distance decreased with increasing maternal weight gains irrespective of maternal presence (Table 3a, estimate \pm se: -0.011 ± 0.004 , $t_{102.20} = -3.137$, $P = 0.0022$), but was independent of offspring weight gains (Table 3a). By contrast, the corrected forceps length was overall larger in males (0.240 ± 0.017

mm) than in females (-0.233 ± 0.012 mm), but independent of maternal presence and the weight gains of the offspring and their mother during family life (Table 3b).

DISCUSSION

Kin competition often reduces and sometimes even entirely negates the benefits of cooperation among relatives (West *et al.* 2002). Surprisingly, however, the role of kin competition between parents and their offspring in the early evolution of parental care has been largely overlooked. Here, we demonstrated that maternal presence under food restriction triggered a local mother-offspring competition in the European earwig *F. auricularia*. This competition manifested itself as a negative effect of high maternal weight gains on the survival of maternally tended (but not maternally deprived) offspring, and positively affected the future reproductive investment of tending mothers. Our results also reveal that the extent of maternal weight gains – and thus the intensity of mother-offspring competition – was highest when mothers had featured a low weight at egg hatching. Finally, we found that maternal presence curtailed the adult body size of those offspring that overcame the lethal consequences of the competition with their mother.

We showed that high maternal weight gains during family life reduced offspring survival until adulthood. Notably, this negative effect (1) was only present in offspring that grew up *with* their mother, (2) arose *after* the end of (i.e. was not detectable during) family life, and (3) was paralleled by a generally lower weight gain of maternally-tended (as compared to maternally-deprived) offspring during family life. Together, these findings demonstrate that mothers competed with their offspring by consuming portions of the limited amount of food available, and thereby indirectly limited the long-term survival prospects of

their progeny, e.g. by increasing the likelihood of offspring starvation or by triggering high levels of siblicide (Dobler & Kölliker 2010). These findings are unlikely to result from the prevention of offspring dispersal in our experimental setup, since nymph dispersal in *F. auricularia* is not accelerated by food limitation (Wong & Kölliker 2012). Hence, our findings emphasize that local competition between parents and their offspring might counteract the benefits of facultative care (Scott & Gladstein 1993; Ward, Cotter & Kilner 2009; Boncoraglio & Kilner 2012) and thus impede the transition to – and the maintenance of – social life in resource-poor environments.

Interestingly, maternal and offspring weight gains interacted in determining the survival of maternally-tended offspring *during* family life: the association between offspring weight gains and survival rates shifted from positive to negative when maternal weight gains were low and high, respectively. This suggests that high offspring weight gains are beneficial when mother-offspring competition is moderate (i.e. when maternal weight gains are low), but costly when it is intense (i.e. when maternal weight gains are high). The first pattern would then indicate that the offsprings' survival mostly relies on their own quality (as reflected by their weight gains) when their mother does not monopolize the food resources. Conversely, the second pattern would indicate that high levels of mother-offspring competition result in a lower amount of left-over food per offspring, which could in turn trigger higher levels of sibling rivalry and siblicide (Dobler & Kölliker 2010; Gardner & Smiseth 2011; Wong, Lucas & Kölliker 2014). Alternatively, this second pattern could reflect filial cannibalism, for instance aimed at increasing the survival prospects of the remaining juveniles (Forbes & Mock 1998; Klug & Bonsall 2007). In both cases, the resulting lower overall offspring survival would increase the *per-capita* amount of food available to – and thus the maximum weight gain

achievable by – the remaining (high-quality) juveniles and their mother. The exact mechanism notwithstanding, our results show that maternal presence under food limitation can reduce offspring fitness even in the short run (see also Thesing *et al.* 2015).

We showed that the initial weight of the mothers, but not the initial weight of their offspring, affected the intensity of mother-offspring competition. Mothers with a low weight at egg hatching gained more weight at the expense of their offspring – and thus reduced their offspring's survival more substantially – than initially heavier mothers. Importantly, maternal weight gains did not differ between clutches of particularly heavy and light nymphs, suggesting that mothers did not adjust the extent of competition in relation to the perceived reproductive value of their offspring (Kilner & Hinde 2012). Together with the observation that offspring overall gained less weight under maternal presence, these findings indicate that the extent of mother-offspring competition is subject to maternal control (Smiseth, Wright & Kölliker 2008; Hinde, Johnstone & Kilner 2010). Note that this holds true although initially heavy nymphs showed lower relative weight gains than initially light nymphs. This is because the above relationship arose independent of maternal presence, indicating that it reflected intrinsic factors such as the genetic quality of family members (Wilson & Nussey 2010) rather than the extrinsic influence of competition. Overall, our findings thus suggest that the (genetic) quality and/or the condition of mothers (see also Koch & Meunier 2014) determine how mothers react to food limitation (e.g. by affecting their responsiveness to offspring solicitation behaviors; Grodzinski & Johnstone 2012) and thus whether they compete with their offspring. Here, mothers of low quality or bad condition might have favored somatic maintenance over self-restraint (McNamara & Houston 1996; Alonso-Alvarez & Velando 2012), either to safeguard their ability to perform crucial parenting behaviors such as predator

defense (Bateson 1994), or in an attempt to shift their investment from current to future offspring (Thorogood, Ewen & Kilner 2011; Kramer & Meunier 2016).

In line with the hypothesis of a condition-dependent shift of maternal investment, we found that high maternal weight gains – and thus intense mother-offspring competition – increased the relative investment into 2nd clutch production among mothers that produced another clutch. Conversely, high maternal weight gains promoted or inhibited the likelihood of 2nd clutch production depending on whether these gains had occurred in concert with high or low offspring weight gains during 1st brood family life, respectively. Finally, we found that the same pattern shaped the length of the inter-clutch interval, but only among mothers that had received a restricted (rather than an *ad libitum*) amount of food after the isolation from their 1st brood offspring. Overall, these findings illustrate that mother-offspring competition might not always trigger a shift in maternal investment from current to future reproduction (Klug *et al.* 2012). This supports the conjecture of an additional motivation for this competition (e.g. the maintenance of maternal condition to perform crucial parenting behaviors; Bateson 1994), which in turn highlights that parent-offspring competition should not uncritically be taken as evidence for parent-offspring conflict (*sensu* Trivers 1974). In particular, some mothers might have heavily invested into their current (low-quality) offspring, thus giving rise to the negative effect of high maternal weight gains on the likelihood of 2nd clutch production in broods featuring low offspring weight gains. This suggests that the scope for conflict might be limited if mothers re-invest competitively acquired resources into their current brood and thereby offset the costs of competition for 1st brood juveniles.

In contrast to its influence on offspring survival and maternal investment into future reproduction, mother-offspring competition did not affect the size and forceps length of

offspring that survived until adulthood. This result suggests that this competition likely does not reflect an *indirect* mechanism of adaptive brood reduction by mothers. Specifically, mother-offspring competition does not seem to have handicapped low-quality offspring to an extent that favored the survival and development of higher-quality offspring, as the average size of maternally-tended offspring should have been larger than that of non-tended juveniles in this scenario (Simmons 1988; Mock & Parker 1997). Nevertheless, our results showed that adults were overall smaller when they had been raised with their mother, a negative effect of maternal presence that has already been found under favorable conditions (featuring unrestricted food access) and that might result from maternal behaviors that are maladaptive under laboratory conditions (such as the burying of food, presumably to prevent microbial growth; see Thesing *et al.* 2015). Our results also revealed that males were overall smaller but had longer forceps than females, confirming the sexual dimorphism of these morphological traits (Radesäter & Halldórsdóttir 1993; Thesing *et al.* 2015). Finally, we showed that body size generally decreased with increasing weight gains of mothers during 1st brood family life. This effect arose independent of maternal presence, indicating that it likely reflected the overall lower initial weight (and thus size) of offspring produced by those mothers that gained a lot of weight during family life rather than the extrinsic influence of competition.

In conclusion, we demonstrated that local competition between parents and their offspring can drastically reduce offspring fitness in species with facultative family life. Parent-offspring competition might thus not only diminish the benefits of a prolonged association of parents with their offspring (Scott & Gladstein 1993), but even impede the evolution of family life altogether. This finding illustrates that parental presence can be associated with costs for the tended offspring (Scott & Gladstein 1993; Meunier & Kölliker 2012; Thesing *et al.* 2015)

that are usually masked by the benefits of parenting behaviors in the wild (Costa 2006; Wong *et al.* 2013), but that emerge whenever the (laboratory) conditions prevent these benefits from taking effect. While parents might be able to reduce the costs of local competition with their offspring under natural conditions, the behavioral changes necessary to do so are likely themselves costly. For example, parents might increase their foraging range (West *et al.* 2002), but will then likely suffer from a higher predation risk (Alonso-Alvarez & Velando 2012). Our results thus generally stress the crucial role of environmental factors such as resource availability and predation pressure in the early evolution of social life. Importantly, our findings also provide a diachronic perspective on social evolution: they suggest that competition between parents and their offspring should decline with an increasing reliance of offspring on parentally provided resources, a process that in turn is known to increase the scope for competition *among* offspring (Gardner & Smiseth 2011). The transition from facultative to obligatory forms of family life might hence be accompanied by a shift in the type of competition that most profoundly affects family interactions.

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RESOURCES

Alonso-Alvarez, C. & Velando, A. (2012) Benefits and costs of parental care. *The evolution of parental care* (eds N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 40–61. Oxford University Press, Oxford.

Bateson, P. (1994) The dynamics of parent-offspring relationships in mammals. *Trends in Ecology & Evolution*, **9**, 399–403.

Boncoraglio, G. & Kilner, R.M. (2012) Female burying beetles benefit from male desertion: Sexual conflict and counter-adaptation over parental investment. *PLoS one*, **7**, e31713.

Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton.

Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.

Costa, J.T. (2006) *The Other Insect Societies*. Harvard University Press, Cambridge.

Cote, J., Clobert, J. & Fitze, P.S. (2007) Mother-offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 9703–9708.

Dobler, R. & Kölliker, M. (2010) Kin-selected siblicide and cannibalism in the European earwig. *Behavioral Ecology*, **21**, 257–263.

- Falk, J., Wong, J.W.Y., Kölliker, M. & Meunier, J. (2014) Sibling cooperation in earwig families provides insights into the early evolution of social life. *The American Naturalist*, **183**, 547–557.
- Forbes, L.S. & Mock, D.W. (1998) Parental Optimism and Progeny Choice: When is Screening for Offspring Quality Affordable? *Journal of Theoretical Biology*, **192**, 3–14.
- Fox, J. (2003) Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, **8**, 1–18.
- Frank, S.A. (1985) Hierarchical Selection Theory and Sex Ratios . II . On Applying the Theory, and a Test with Fig Wasps. *Evolution*, **39**, 949–964.
- Gardner, A. & Smiseth, P.T. (2011) Evolution of parental care driven by mutual reinforcement of parental food provisioning and sibling competition. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 196–203.
- Grodzinski, U. & Johnstone, R.A. (2012) Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 109–15.
- Harrison, X.A. (2015) A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ*, **3**, e11114.
- Hinde, C.A., Johnstone, R.A. & Kilner, R.M. (2010) Parent-offspring conflict and coadaptation. *Science (New York, N.Y.)*, **327**, 1373–6.
- Kilner, R.M. & Hinde, C.A. (2012) Parent-offspring conflict. *The Evolution of Parental Care*

- (eds N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 119–132. Oxford University Press, Oxford.
- Klug, H., Alonso, S.H. & Bonsall, M.B. (2012) Theoretical foundations of parental care. *The Evolution of Parental Care* (eds N. Royle, M. Kölliker & P.T. Smiseth), pp. 21–39. Oxford University Press, Oxford.
- Klug, H. & Bonsall, M.B. (2007) When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. *The American Naturalist*, **170**, 886–901.
- Klug, H. & Bonsall, M.B. (2010) Life history and the evolution of parental care. *Evolution*, **64**, 823–35.
- Koch, L.K. & Meunier, J. (2014) Mother and offspring fitness in an insect with maternal care: phenotypic trade-offs between egg number, egg mass and egg care. *BMC Evolutionary Biology*, **14**, 125.
- Kölliker, M. (2007) Benefits and costs of earwig (*Forficula auricularia*) family life. *Behavioral Ecology and Sociobiology*, **61**, 1489–1497.
- Kölliker, M. & Vancassel, M. (2007) Maternal attendance and the maintenance of family groups in common earwigs (*Forficula auricularia*): a field experiment. *Ecological Entomology*, **32**, 24–27.
- Kramer, J., Körner, M., Diehl, J.M.C., Scheiner, C., Yüksel-Dadak, A., Christl, T., Kohlmeier, P. & Meunier, J. (2017) Data from: When earwig mothers do not care to share: parent-offspring competition and the evolution of family life. *Dryad Digital Repository*. doi:10.5061/dryad.651ss

- Kramer, J. & Meunier, J. (2016) Maternal condition determines offspring behavior toward family members in the European earwig. *Behavioral Ecology*, **27**, 494–500.
- Kramer, J., Thesing, J. & Meunier, J. (2015) Negative association between parental care and sibling cooperation in earwigs: a new perspective on the early evolution of family life? *Journal of Evolutionary Biology*, **28**, 1299–1308.
- Krause, J. & Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press, Oxford.
- Lamb, R.J. (1976a) Dispersal by nesting earwigs, *Forficula auricularia* (Dermaptera: Forficulidae). *The Canadian Entomologist*, **108**, 213–216.
- Lamb, R.J. (1976b) Parental behavior in the Dermaptera with special reference to *Forficula auricularia* (Dermaptera: Forficulidae). *The Canadian Entomologist*, **108**, 609–619.
- McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.
- Meunier, J. & Kölliker, M. (2012) When it is costly to have a caring mother: food limitation erases the benefits of parental care in earwigs. *Biology Letters*, **8**, 547–550.
- Meunier, J. & Kölliker, M. (2013) Inbreeding depression in an insect with maternal care: influences of family interactions, life stage and offspring sex. *Journal of Evolutionary Biology*, 1–12.
- Meunier, J., Wong, J.W.Y., Gómez, Y., Kuttler, S., Röllin, L., Stucki, D. & Kölliker, M. (2012) One clutch or two clutches? Fitness correlates of coexisting alternative female life-histories in the European earwig. *Evolutionary Ecology*, **26**, 669–682.
- Mock, D.W. & Parker, G.A. (1997) *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.

- Radesäter, T. & Halldórsdóttir, H. (1993) Fluctuating asymmetry and forceps size in earwigs, *Forficula auricularia*. *Animal Behaviour*, **45**, 626–628.
- Roulin, A. & Dreiss, A.N. (2012) Sibling competition and cooperation over parental care. *The Evolution of Parental Care* (eds N.J. Royle, P.T. Smiseth & M. Kölliker), pp. 133–149. Oxford University Press, Oxford.
- Royle, N.J., Smiseth, P.T. & Kölliker, M. (eds). (2012) *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Scott, M.P. & Gladstein, D.S. (1993) Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. *Evolutionary Ecology*, **7**, 362–378.
- Simmons, R. (1988) Offspring quality and the evolution of cainism. *Ibis*, **130**, 339–357.
- Smiseth, P.T., Darwell, C.T. & Moore, A.J. (2003) Partial begging: an empirical model for the early evolution of offspring signalling. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1773–1777.
- Smiseth, P.T., Wright, J. & Kölliker, M. (2008) Parent-offspring conflict and co-adaptation: behavioural ecology meets quantitative genetics. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1823–1830.
- Sorato, E., Griffith, S.C. & Russell, A.F. (2016) The price of associating with breeders in the cooperatively breeding chestnut-crowned babbler: foraging constraints, survival and sociality. *Journal of Animal Ecology*, **85**, 1340–1351.
- Staerkle, M. & Kölliker, M. (2008) Maternal food regurgitation to nymphs in earwigs

- (Forficula auricularia). *Ethology*, **114**, 844–850.
- Thesing, J., Kramer, J., Koch, L.K. & Meunier, J. (2015) Short-term benefits, but transgenerational costs of maternal loss in an insect with facultative maternal care. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151617.
- Thorogood, R., Ewen, J.G. & Kilner, R.M. (2011) Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2638–2645.
- Trivers, R.L. (1974) Parent-offspring conflict. *American Zoologist*, **14**, 249–264.
- Ward, R.J.S., Cotter, S.C. & Kilner, R.M. (2009) Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*. *Behavioral Ecology*, **20**, 1274–1281.
- West, S.A., Murray, M.G., Machado, C.A., Griffin, A.S. & Herre, E.A. (2001) Testing Hamilton's rule with competition between relatives. *Nature*, **409**, 510–513.
- West, S.A., Pen, I. & Griffin, A.S. (2002) Cooperation and competition between relatives. *Science (New York, N.Y.)*, **296**, 72–75.
- Wilson, E.O. (1975) *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge.
- Wilson, A.J. & Nussey, D.H. (2010) What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, **25**, 207–214.
- Wong, J.W.Y. & Kölliker, M. (2012) The effect of female condition on maternal care in the European earwig. *Ethology*, **118**, 450–459.
- Wong, J.W.Y., Lucas, C. & Kölliker, M. (2014) Cues of Maternal Condition Influence Offspring

Selfishness. *PloS ONE*, **9**, e87214.

Wong, J.W.Y., Meunier, J. & Kölliker, M. (2013) The evolution of parental care in insects: the roles of ecology, life history and the social environment. *Ecological Entomology*, **38**, 123–137.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Rearing protocol

Table S1. Results of the full model analyzing offspring survival

Appendix S2. Correction of forceps length

Appendix S3. Correction of offspring weight at hatching

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Table 1 | Offspring survival. Influence of maternal presence, and the relative weight gain of mothers and their offspring on the offsprings' survival (a) upon adult emergence and (b) at the end of family life. Significant P-values are given in bold print ([§] values as indicated before removal of the interaction from the model).

	offspring survival			
	(a) upon adult emergence		(b) at the end of family life	
	Wald χ_1^2	P	Wald χ_1^2	P
maternal presence (MP)	51.92	< 0.0001	4.67	0.0306
offspring weight gain (OWG)	23.61	< 0.0001	1.49	0.2228
maternal weight gain (MWG)	1.21	0.2711	< 0.01	0.9735
MP : MWG	4.56	0.0327	0.14	0.7085
MP : OWG	6.84	0.0089	0.92	0.3383
MWG : OWG	1.56 [§]	0.2114 [§]	0.02	0.9029
MP: MWG : OWG	2.35 [§]	0.1255 [§]	7.00	0.0082

Table 2 | Maternal investment into 2nd clutch production. Influence of maternal weight gains, offspring weight gains, and the food availability after family life (high or low food) on (a) the likelihood of 2nd clutch production, (b) the length of the inter-clutch interval, and (c) the relative investment into 2nd clutch production. Significant P-values are given in bold print ([§] values as indicated before removal of the interaction from the model).

	(a) likelihood of production		(b) inter-clutch interval		(c) relative investment	
	LR χ_1^2	P	F ₁	P	LR χ_1^2	P
maternal weight gain (MWG)	0.01	0.9177	0.28	0.5962	5.39	0.0203
offspring weight gain (OWG)	2.03	0.1546	0.05	0.8285	2.18	0.1399
food availability (FA)	3.70	0.0544	4.49	0.0388	4.10	0.0429
MWG : OWG	10.19	0.0014	0.13	0.7172	0.80 [§]	0.3712 [§]
MWG : FA	2.77 [§]	0.0961 [§]	0.02	0.8967	0.03 [§]	0.8607 [§]
OWG : FA	1.11 [§]	0.2921 [§]	0.12	0.7302	1.00 [§]	0.3185 [§]
MWG : OWG : FA	0.48 [§]	0.4904 [§]	7.32	0.0092	0.02 [§]	0.8950 [§]
type of model sample size	GLM 112		LM 61		GLM 61	

Table 3 | Morphology of the surviving adult offspring. Influence of maternal presence, offspring sex, and the weight gains of nymphs and their mother during family life on (a) the eye distance and (b) the (corrected) forceps length of the surviving adult offspring. Significant P-values are given in bold print (^s values as indicated before removal of the interaction from the model).

	(a) eye distance		(b) forceps length	
	Wald χ_1^2	P	Wald χ_1^2	P
maternal presence	6.16	0.0131	0.69	0.4075
sex	59.51	< 0.0001	659.51	< 0.0001
maternal weight gain	9.84	0.0017	0.69	0.4075
offspring weight gain	0.37	0.5423	1.97	0.1608

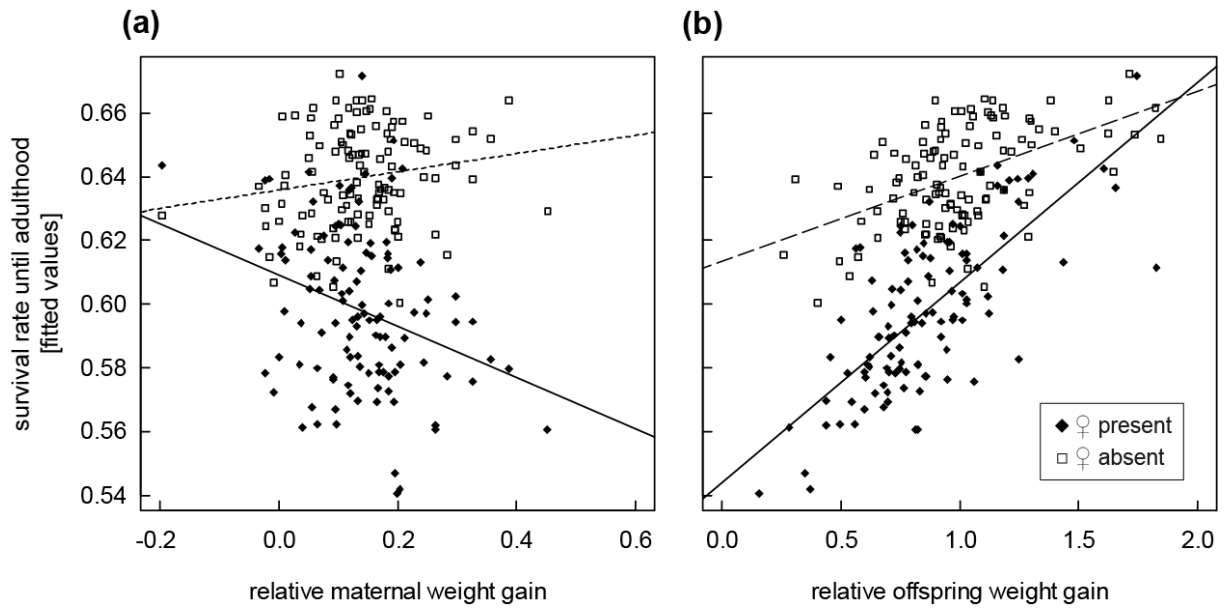


Figure 1 | Offspring survival until adulthood. Influence of (a) the relative weight gain of mothers and (b) the relative weight gain of their offspring on offspring survival until adulthood under maternal presence (filled squares) and absence (empty squares).

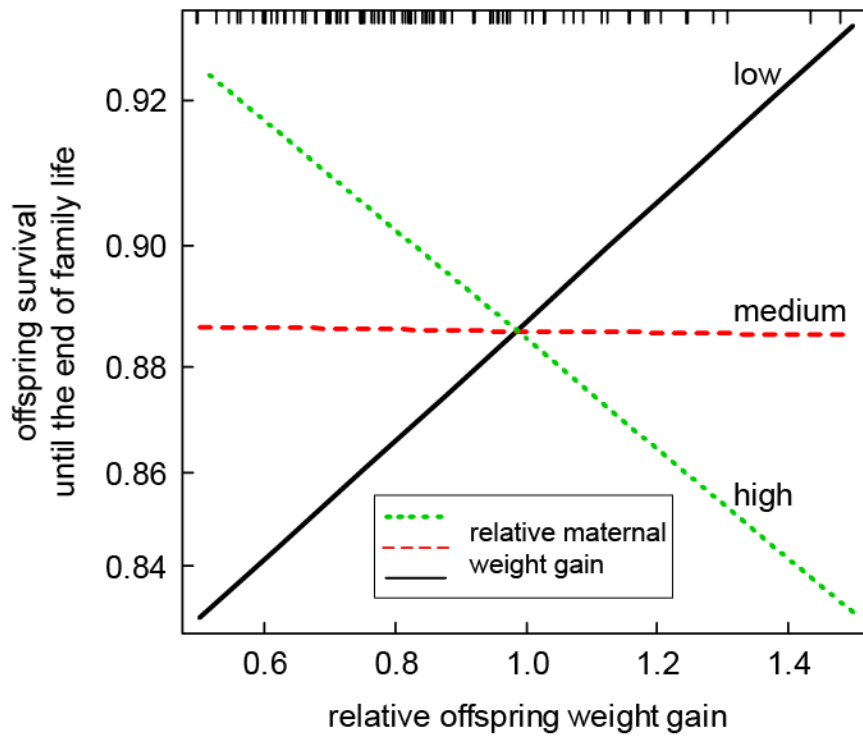


Figure 2 | Interactive effect of maternal and offspring weight gains on the survival of maternally tended offspring during family life. To illustrate the interaction, regression lines are given for an average value of maternal weight gains (median = 0.13; dashed line), as well as for a comparatively low (1st quantile = 0.07; solid line) and high (3rd quantile = 0.20; dotted line) weight gains, respectively.

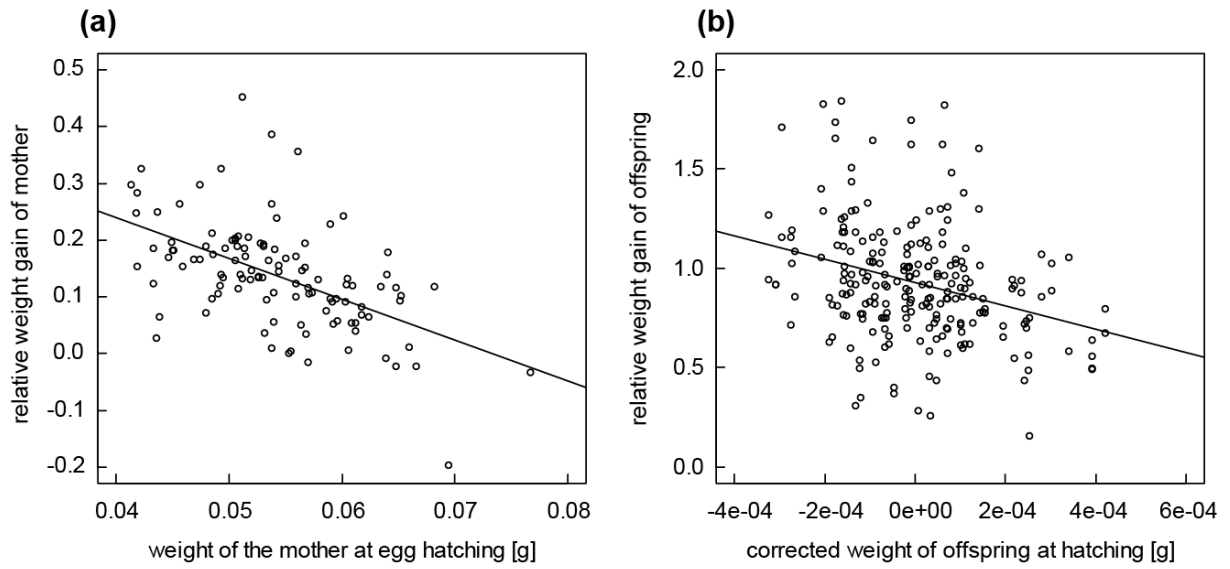


Figure 3 | Weight gains and initial weight. Influence of (a) the weight of mothers and (b) the weight of nymphs at egg hatching (corrected for the weight of their mother; see above) on their respective weight gains during family life.

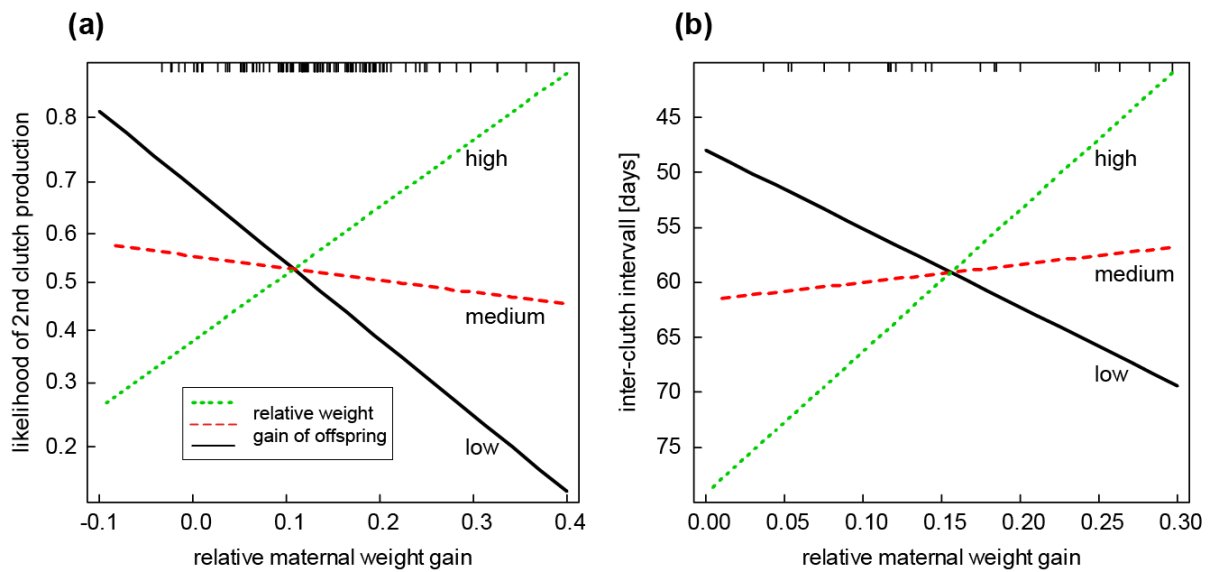


Figure 4 | Interactive effects of maternal and offspring weight gains on 2nd clutch traits.

Depicted are the interactive effects of maternal and offspring weight gains on (a) the likelihood of 2nd clutch production among all mothers, as well as on (b) the length of the inter-clutch interval among those mothers with restricted food access after family life. To illustrate the interactions, regression lines are given for an average value of offspring weight gains (median = 0.82; dashed line), as well as for a low (1st quantile = 0.64; solid line) and a high value (3rd quantile = 1.03; dotted line), respectively. Note that the axis depicting the inter-clutch interval is reversed as shorter intervals likely reflect higher maternal fitness.