Sex-specific negotiation rules in a costly conflict over parental care

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Abstract

Sexual conflict theory predicts a trade-off in individual parental care allocated to either current or future reproduction. The optimal amount of current parental effort is expected to differ between adult males and females, with a conflict resolution being reached by negotiation depending on multiple family cues. Currently, a debate exists on how negotiation takes place, along with its potential costs or benefits for all family members. In particular, the specific negotiation rules that male and female parents apply often remain obscure, which in part results from a shortage of empirical studies. We used captive canaries, *Serinus canaria*, to evaluate consequences of sexual conflict for the offspring by comparing uniparental (female cared for a half clutch) and biparental (both parents cared for a full clutch) families. Our results suggest overall less parental effort in biparental families and offspring were observed to beg harder for parental resources, weigh less as fledglings and tended to grow slower compared to uniparental families. To further increase our understanding of parental negotiation rules, we manipulated the degree of partner visibility and thus information about partner effort by temporarily splitting biparental families. Male and female provisioning strategies depended on both partner visibility and brood demand. An increase in male provisioning was observed after mate removal, whereas the opposite pattern was observed in females. Females, however, increased provisioning in response to offspring begging. We conclude that (1) sexual conflict over parental care is costly for the offspring, (2) sex-specific negotiation rules exist and probably relate to an asymmetry in gathered information and (3) changes in parental feeding strategies trigger a feedback mechanism via brood demand, highlighting the need to consider all family members in order to understand family conflicts and their potential resolution.

**Key words:** negotiation, offspring begging, parental care, parental provisioning, sexual conflict
Introduction

Sexual conflict is expected to arise when males and females have different fitness optima for a given trait and do not reach these optima simultaneously (Arnqvist & Rowe 2005). Previous studies on sexual conflict, along with its causes, consequences and role in speciation (Parker & Partridge 1998; Arnqvist et al. 2000), have mainly focused on a battle prior to zygote formation (Parker 2006). However, sexual conflict after zygote formation is receiving increased research interest (reviewed in Royle et al. 2012). In particular, the role of negotiation between parents in how conflict over the amount of parental care provided for the offspring can be resolved (Lessells 2012) has been the focus of attention since Trivers (1972) started the evolutionary discussion on the limited harmonization that exists between parents.

The essence of sexual conflict over parental care is captured in a trade-off between current and future reproduction for each parent (Houston et al. 2005). Care results in a clear benefit for the offspring and inherently increases the fitness of both parents, but each parent only has to pay the cost of its own contribution (Royle et al. 2012). In most cases, it is therefore in each parent’s interest to limit its own effort and leave the highest workload for its mate. None the less, biparental care is observed in a taxonomically diverse range of species (Royle et al. 2012), with an overall increased number of offspring reared being the main benefit over uniparental care (Smith & Härdling 2000; Royle et al. 2006). Indeed, once biparental care has evolved, subsequent coevolution of male and female parental behaviour may result in one parent becoming unable to care for the entire brood alone (Houston & Davies 1985; Lessells 2012). How sexual conflict is resolved and to what extent each parent should provide care have been central themes of numerous mathematical models (Lessells 2012) and empirical studies (reviewed by Harrison et al. 2009).

The classic ‘sealed bid’ game-theoretical approach of Houston & Davies (1985) suggested that each parent benefits by exploiting its partner’s effort until an evolutionarily stable level
of care is established. This model assumed fixed levels of individual effort, despite flexibility in care behaviour being observed in response to changed partner effort (Harrison et al. 2009). This has triggered the development of models to include such flexibility, or negotiation in ‘behavioural time’ (McNamara et al. 1999, 2003). Each parent is expected to adjust its effort in response to its partner by monitoring each other’s activity pattern (Hinde 2006; Johnstone et al. 2014) or the condition of the brood (Hinde & Kilner 2007; Lessells & McNamara 2012) in a series of alternated bids (or bouts). It became clear that selection acts on a parent’s behavioural response to its mate’s behaviour (McNamara et al. 1999), rather than on a specific level of parental effort per se (Houston & Davies 1985). As a result of evolved negotiation rules, parents may be able to exploit their mate, perhaps even by handicapping themselves (Barta et al. 2002; Houston et al. 2005). Ultimately, this theory predicts that negotiation could result in offspring faring worse under biparental care, implying a cost of sexual conflict (Royle et al. 2002, 2006; Lessells & McNamara 2012). Recent observations in great tits, Parus major, however, suggest a completely opposite pattern in which parents appear to match each other’s investment, resulting in more turn taking and high brood visit rates (Johnstone & Hinde 2006; Hinde 2006). These controversial observations inspired an alternative negotiation model (Johnstone et al. 2014), which contrarily predicts enhanced offspring fitness driven by behavioural coordination between parents that acts as a form of reciprocity and reduces sexual conflict. Taken together, the theoretical models on conflict resolution by negotiation described above predict contrasting consequences for the offspring. Empirical tests for such consequences are limited to a single study with captive zebra finches, Taeniopygia guttata (Royle et al. 2002, 2006). Furthermore, altered provisioning behaviour in response to changed partner effort is expected to trigger a dynamic feedback mechanism with offspring begging behaviour (Morales & Velando 2013). Thus parental negotiation rules may result not only from sexual
conflict over care, but also from changes in offspring behaviour (Parker et al. 2002b; Smiseth et al. 2008; Thorogood et al. 2011). Therefore, empirical studies are urgently needed to fill this knowledge gap on the mechanisms and consequences of parental negotiation, without neglecting the multiple family cues that each parent may use to gain information (Houston et al. 2005; Hinde & Kilner 2007).

Studies addressing this topic have typically examined the change in parental effort when a focal bird’s mate was either experimentally removed or handicapped (e.g. by feather clipping or adding weights) in comparison with biparental control families (Sasvári 1986; Harrison et al. 2009). A variety of behavioural responses have been reported, but partial compensation was the most general outcome. Although such studies confirm a certain degree of individual responsiveness towards their partners, two major concerns arise: first, mate handicapping techniques are likely to change the perception of partner quality, so any observed change in response behaviour may be attributed not solely to changed parental effort, but also to lowered mate attractiveness (i.e. differential allocation, Sheldon 2000). Second, most of these studies say little about the consequences of changes in parental strategies for offspring, and thus the potential costs of negotiation. None the less, the overview of Harrison et al. (2009) revealed two important insights, namely potential differences in both response behaviour between the sexes (Griggio & Pilastro 2007) and between manipulation methods. Sexual differences in parental care do occur and are generally explained in an evolutionary context related to uncertainty of parentage, anisogamy and population sex ratio (Kokko & Jennions 2012). Although often neglected in mathematical models, sexual differences in negotiation over parental care are also expected. For instance when costs and/or benefits of parental care differ between males and females (Cezilly 1993; Sanz et al. 2000), but especially when both sexes gather information differently about the brood’s need and the partner’s work effort (Johnstone & Hinde 2006). In great tits for example, female parents may be better informed
as they spend more time with the young, compared to males which invest more time in
territory defence (Sanz et al. 2000). The better informed parent is then predicted to work
harder, respond more strongly to changes in brood need and compensate more strongly for
changes in partner effort (Johnstone & Hinde 2006). An elegant method to investigate such
parental negotiation rules depending upon available information entails experimental
manipulations of breeding pairs in a reversible way and in a range of treatment levels
(Houston et al. 2005). Indeed, the overview of Harrison et al. (2009) clearly indicated more
compensatory behaviour in (permanent) mate removal, relative to mate handicapping
experiments. Temporarily removing and reversibly restraining parents from providing full
care or information gathering may offer a fruitful research tool to assess the informative cues
that are important for applying parental negotiation rules.

Our aims were threefold. First, we investigated the consequences of negotiation by
comparing offspring development in biparental (both parents care for a full clutch) and
uniparental (female cares for a half clutch) families. Theoretical models predict negative
(Lessells & McNamara 2012) or positive (Johnstone et al. 2014) consequences for the
offspring, although empirical evidence is especially limited (Royle et al. 2002, 2006).
Second, we aimed to gain innovative insights into the applied negotiation rules of both
parents by temporarily manipulating the amount of information that each parent could gather
from their partner (Johnstone & Hinde 2006; Harrison et al. 2009). We therefore measured
male and female behavioural responses when their partner was temporarily restrained in
providing direct care. This was done in a set-up in which the partner was either visible or
invisible and thus with a different degree of potentially perceived information on partner
work effort. We expected a partial compensation response to be stronger when the partner
was invisible (cf. mate removal, Harrison et al. 2009), with potential differences between the
sexes. Finally, we simultaneously investigated offspring begging intensity, as this may form a
feedback mechanism that may impinge on parental provisioning strategies (Morales & Velando 2013). We expected that the better informed sex may respond more strongly to changes in brood need (Johnstone & Hinde 2006).

**Methods**

We used 26 male and 26 female adult Fife Fancy canaries, *Serinus canaria*, for the experiment, originating from our own laboratory stock population. All birds were unrelated first-year canaries. From 15 March 2012 onwards, males were housed in individual cages (50x64 cm and 40 cm high, GEHU cages, Nijverdal, The Netherlands) for territorial establishment and females were housed in one large internal aviary (2x2x2m). All birds experienced a long light regime (14:10 h light:dark) and had access to seeds and water ad libitum. Egg food was provided twice a week. After 5 weeks of long light regime, all birds were paired by randomly allocating females to the male cages and nesting materials were provided. Progress on nest building, egg laying and incubation was monitored daily. We synchronized hatching within broods by keeping the first two eggs at room temperature (20 °C) and returning them after the third egg was laid. This minimized within-brood differences in size facilitating cross-fostering (Hinde et al. 2009; Estramil et al. 2013). At hatching (day 0), chicks were individually marked with a unique within-nest colour on their back, using nontoxic pens (Artline70N) which was reapplied when necessary. From then onwards, egg food and germinated seeds were provided on a daily basis. Chicks were ringed with a unique code on day 7. The research was approved by the Ethical Committee of the University of Antwerp (ID: 2011-86).
Experimental set-up

Nests were alternately assigned to uniparental and biparental families ($N = 13$ nests per family treatment; $N = 78$ chicks) on day 2. Meanwhile, chicks were cross-fostered to ensure that any observed variation in chick begging and parental feeding was not attributed to experience with their biological parents after hatching (Estramil et al. 2013). Cross-fostering occurred as follows: nests of four chicks were split into two pairs, one chick pair being cross-fostered to a uniparental nest to be raised by a female alone and the other cross-fostered to a biparental nest. Biparental nests received two pairs of nestlings, to match an equal number of chicks per adult and thus to apply a comparable workload per parent in both groups (Royle et al. 2002, 2006). Only adult females were used in the uniparental group, because males do not engage in brooding and were thus not expected to successfully raise the offspring on their own. Nests were video recorded for almost 2 h (mean ± 1SE: 108.7 ± 0.3 min) on days 9 and 12 (uniparental families) and days 9, 10 and 12 (biparental families) to assess parental feeding and chick begging behaviours (for details see below). An additional manipulation was performed in biparental nests: on days 10 and 12 the nests were temporarily split so that each parent had to take care of two nestlings alone in a separate cage unit. On one of these days, cages were placed opposite to and in contact with each other, so that the adults could see into each other's nest and communicate with each other through the bars (visible partner manipulation). On the other day, the cages were placed in two separate, identical rooms (invisible partner manipulation), to exclude all visible and auditory contact between the parents. The order of these manipulations was randomized between nests and alternated within nests. This set-up enabled us to assess (1) effects of family structure on offspring development, (2) differences in parental provisioning effort and chick begging behaviour between uni- and biparental families on day 9 and (3) differences in temporarily split
biparental groups due to partner visibility on days 10 and 12 in biparental groups and (4) to compare female effort in uniparental and split biparental families on day 12.

**Chick begging and parental provisioning behaviour**

We used the summed duration of all observed feeding bouts in all analyses as a proxy for parental provisioning effort, with each individual chick being the experimental unit. Each time begging was observed, nestling begging intensity was estimated as in Kilner (2001). Briefly, an intensity score ranging from 1 (i.e. motionless nestling only with open gape) to 4 (gape open, head back, neck stretched and back vertical) was noted for each second that begging was observed in the video fragment. Total begging effort was calculated as the sum of all scores over the duration of begging. Finally, begging reward was calculated as the total begging intensity divided by the number of parental feeds received. All videos were analysed using The Observer XT software (Noldus Information Technology, Wageningen, The Netherlands) and all provisioning and begging estimates were corrected for the duration of the recorded video. The latter was done by dividing the total time of the observed behaviour (min) by the length of the video (h).

**Nestling development and molecular sex determination**

Chicks were weighed daily from day 0 until day 14. Individual chick growth rate was estimated as the regression slopes of chick body mass against age during the linear phase of the growth curve (i.e. first 14 days). Growth rate determined via nonlinear Gompertz curves gave very similar estimates (Pearson correlation: $r_{50} = 0.97$, $N = 52$, $P < 0.0001$). Furthermore, body mass and tarsus length were measured at day 20 (i.e. at the fledgling
Independence is reached at the age of 30 days, at which time chicks are no longer fed by their parents. On this day, final chick body mass was measured and a blood sample (50 µl) was collected from the alar wing vein for molecular sex determination. DNA was extracted from red blood cells using Chelex resin-based DNA extraction (Walsh et al. 1991) or Qiagen DNeasy kit methods applying the manufacturer’s protocol. CHD genes were amplified by PCR using the protocol of Griffiths et al. (1998). The amplified PCR product was separated on a 1.5% agarose gel stained with ethidium bromide. Males were identified as having a single CHD-Z band whereas females also have a CHD-W band.

Statistical analysis

Separate linear mixed models were applied to test for differences in chick development (growth rate, body mass at day 20 and 30 and tarsus length) between family treatments (uniparental and biparental). Additional mixed models were performed for body mass, but corrected for size by adding tarsus length as an extra explanatory variable. Similar linear mixed models were performed to test for behavioural differences (total begging intensity, begging reward and parental feeding effort) between uniparental and biparental families on day 9. Family treatment, chick mass and their interaction were added to the model as explanatory variables. Finally, in a mixed model using backward stepwise elimination, we tested whether male and female parents differed in parental provisioning effort during the visibility manipulation (day 10 and day 12). Explanatory variables in this model include experimental manipulation (visible or invisible partner), chick weight and chick begging intensity, along with feeding sex as the main effect and as an interaction with all former parameters. Total begging intensity and parental feeding effort had to be square root-transformed to meet assumptions for normality. Given the genetic similarities among
nestlings within the original nest before cross-fostering and the similar environmental conditions within each foster nest, both original nest ID and foster nest ID were added as independent random factors to all these models to adjust for a bias in statistical independence. Tests for potential sex differences in nestling development and biased provisioning towards male or female chicks are presented in the Appendix. All analyses were performed in SAS 9.3 (SAS Institute Inc., Cary, NC, U.S.A.). Significant findings are indicated by $P<0.05$, tendencies by $P<0.10$ and nonsignificant results by $P>0.1$. Means ± 1 SE are presented throughout the results.

Results

Comparison of uni- and biparental families

Nestling development

Several marked differences were observed between chicks raised in different family treatments. Chicks from uniparental families were significantly heavier, both absolute (17.76 ± 0.50 g versus 15.97 ± 0.36 g; $F_{1,36} = 8.56, P = 0.006$; Fig. 1a) and corrected for tarsus length ($F_{1,35} = 11.16, P = 0.002$) at fledging and tended to grow faster (0.60 ± 0.04 g/day versus 0.55 ± 0.04 g/day; $F_{1,37} = 2.99, P = 0.092$) than chicks raised in biparental nests. Similar patterns were observed for size-corrected body mass at independence ($F_{1,19} = 4.47, P = 0.048$).

Chick begging and parental provisioning (day 9)
Chick begging behaviour and parental provisioning effort both differed strongly between family treatments. Specifically, parental feeding effort was much lower in biparental families (10.2 ± 1.8 min/h versus 24.2 ± 5.7 min/h; $F_{1,35} = 7.56, P = 0.009$; see Fig. 1b) and was biased towards heavier chicks ($F_{1,35} = 14.53, P = 0.0005$). On the other hand, begging intensity was significantly higher in biparental than uniparental families (respective scores: 783.0 ± 40.0 versus 509.4 ± 34.0; $F_{1,36} = 8.27, P = 0.007$; see Fig. 1c), which was independent of the chicks’ individual weight ($F_{1,35} = 0.0, P = 0.95$). As a consequence, begging reward was also much higher in the uniparental treatment ($F_{1,36} = 23.74, P < 0.0001$). Across treatments, offspring body mass had similar effects on both provisioning (interaction term: $F_{1,34} = 2.57, P = 0.12$) and begging ($F_{1,34} = 0.09, P = 0.77$) behaviour.

**Visibility manipulation (day 10 and 12)**

The visibility manipulation experiment in the temporarily split biparental groups enabled us to disentangle male and female provisioning strategies. Parental feeding effort increased towards heavier chicks at a comparable rate for male and female parents (Table 1). Similarly, feeding effort increased with chick begging intensity, but with a higher responsiveness to begging in females than males (Table 1). Parents differed in provisioning effort depending on the visibility of the partner. Specifically, male parents provided more food than female parents and this sexual difference was even more pronounced when the partner was invisible, relative to the visible set-up (see Table 1, Fig. 2). A post hoc test revealed that especially males increased their workload when their partner became invisible (20.1 ± 0.5 min/h; $t_{59} = 2.04, P = 0.046$), whereas females tended to decrease their feeding effort in such conditions (2.8 ± 0.5 min/h; $t_{59} = -1.80, P = 0.077$; see Fig. 2). Furthermore, no significant differences in food provisioning were observed between males (13.0 ± 0.5 min/h) and females (6.7 ± 0.6
min/h) in the visible set-up ($t_{59} = -1.51, P = 0.14$), which strongly contrasts with the invisible set-up ($t_{59} = -4.67, P < 0.0001$). In addition, female provisioning effort towards chicks measured on day 12 was almost two times lower during the invisible manipulation compared to chicks from uniparental families on the same day ($F_{1,18} = 12.0, P = 0.003$).

### Discussion

Our results support the existence of a costly sexual conflict over parental care. Offspring from biparental families were observed to beg harder for parental resources, to weigh less as fledglings and to tend to grow more slowly than uniparental families, despite similar parental workloads. We further presented empirical evidence that these costs may relate to negotiation and showed how males and females differ in their negotiation rules. The latter depended on the available information on brood begging intensity and the mate’s work effort. Below we explain in detail how these results fit within the current theoretical framework of sexual conflict over care and discuss the implications for other forms of family conflicts and their resolution.

### Cost of sexual conflict

Current theory on conflict resolution in species with biparental care predicts that each parent is able to adjust the amount of care in response to its partner’s effort: a behavioural response called negotiation (McNamara et al. 1999). Despite a shortage of empirical tests, a current debate exists on how negotiation takes place (Lessells 2012) along with its potential costs (Lessells & McNamara 2012) or benefits (Johnstone et al. 2014) for the offspring (Royle et al. 2002, 2006). Likewise, such offspring consequences are commonly neglected in mate
removal and handicapping studies (Harrison et al. 2009). Our results indicate that, when controlling for an equal potential workload, parental provisioning effort towards each offspring was only half as much in biparental nests compared to females caring alone, despite higher offspring begging intensity in biparental nests. Furthermore, chicks from biparental nests tended to grow more slowly and weigh significantly less as fledglings and at independence, indicating lowered competitive abilities early in life. These results are generally in line with a study on captive zebra finches, *Taeniopygia guttata*, which similarly found less parental investment and less predictable food delivery in biparental nests (Royle et al. 2006) and even a decrease in attractiveness of male chicks later in life (Royle et al. 2002). To our knowledge, these are the only empirical studies that support a cost of sexual conflict through negotiation over parental care as predicted by Lessells & McNamara (2012), and which, however, are opposite to Johnstone et al.’s (2014) expectations.

If negotiation is indeed costly, one may then question why parents do not divide tasks and care for only some of the offspring (Lessells 2002). Several taxon-specific hypotheses suggest benefits of larger brood size (e.g. through thermoregulation) or inextricable task division between the sexes (Lessells 2012). Our results may add another argument to this discussion and suggest that an additional benefit of biparental care throughout an individual’s life may be overall increased offspring quantity, rather than quality, at least in some songbirds (Smith & Härdling 2000; Royle et al. 2006). Specifically, we indicate that uniparental females may opt to invest more in the quality of the current brood when they rely only on themselves at the onset of the breeding period. This increased current investment is expected to lower the female’s general condition and may therefore be at the expense of future reproductive investment and lifetime fitness (Trivers 1972; Royle et al. 2002). Such trade-offs remain speculative and require further attention, but they may well hamper the evolution of uniparental care.
**Sex-specific negotiation rules**

Our visibility manipulation revealed that the ability to observe the partner’s activity pattern and characteristics of the brood are important cues for parents to provide care (Hinde & Kilner 2007). Moreover, males and females varied strongly in the cues used to define their provisioning response, depending on both the degree of partner visibility and offspring begging intensity. In detail, parents did not differ significantly in provisioning when mates were visible to each other, although without the option to provide direct help. However, an interesting sexual difference became explicit when mates were out of sight from each other, with males showing increased and females decreased feeding effort. Such sexual differences in negotiation rules may relate to an asymmetry in gathered information between the sexes (Johnstone & Hinde 2006). Indeed, male and female canaries generally differ in provisioning strategy (Kilner 2002), whereby females spend more time near the nest, invest less effort in foraging and frequently receive food via allofeeding (Estramil 2014). This task division probably leads to an asymmetry in information about partner work effort in favour of the females (Johnstone & Hinde 2006). Mathematical models and observations in great tits indicated that the parent better informed about the brood’s need is expected to respond more strongly to changes in offspring demand, work harder and compensate more strongly for changes in partner effort (Johnstone & Hinde 2006). Females indeed appeared more sensitive to offspring begging intensity (see also Kilner 2002). However, our observations are in contrast with the last of these predictions, as our results suggest that well-informed females do not work harder but keep private information and exploit their partner when they are out of sight. Why females do not exploit their mate permanently is likely to depend on the balance between mate exploitation and the female’s urge to respond to increased offspring begging behaviour.
Recent observations by Johnstone et al. (2014) indicated a form of cooperation between great tit parents with turn taking in provisioning speeding up their feeding rate. We believe that the contrasting findings may result from species-specific differences in the adequacy of information gathering about partner effort. For example, the variation in caterpillar size delivered by great tit parents (single-load species) is probably smaller than the variation in amount of seeds collected and processed by canary parents (multiload species). This may create a greater potential for cheating by the best informed parent in multiload species. Such species-specific differences in information gathering may provide a promising future research avenue. We therefore suggest a comparative study including a range of species with different foraging strategies should be performed with an experimental set-up similar to ours.

**Integrated family conflicts**

Food provisioning towards each chick was lowered when both parents cared for their young. It is therefore not surprising that we found amplified begging behaviour in biparental nests. However, it remains unknown whether increased begging of biparental nestlings is the cause or the consequence of suboptimal provisioning. On the one hand, offspring may increase begging in response to their hunger status and thus as a reflection of slower development. On the other hand, our results may also imply that parental negotiation results in greater sibling competition and begging, which on its own can lead to a decrease in offspring condition and growth (Kilner 2001; Royle et al. 2006). As confirmed earlier in canaries, sibling conflict over care through begging may be energetically demanding, resulting in less resource allocation towards growth (Kilner 2001). Furthermore, predictive models in parent–offspring conflict theory incorporate costs of begging behaviour to maintain evolutionary stability (Parker et al. 2002a). Without costs, begging would escalate without bounds. Whatever the cause or consequence might be of poorer condition on increased biparental nestling begging,
the bottom line is that parental negotiation rules may affect chick begging behaviour, which
in turn is traded off against offspring growth and body mass. Parents, and here in particular
mothers, do not only respond to their mate’s effort. Our results also indicate the importance
of chick begging behaviour (Parker et al. 2002a) and chick mass (Lessells & McNamara
2012) as determinants in providing care, and this closes the cycle of intrafamilial dynamics.
Our results therefore underline the importance of investigating joint interactions among all
family members (Hinde & Kilner 2007; Smiseth et al. 2008; Morales et al. 2009; Hinde et al.
2010) as indicated by our observed direct influence of sexual conflict over parental care on
offspring behaviour.

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Appendix
Differences between male and female offspring

In this appendix we describe how we tested for potential sex differences in chick development and for biased provisioning towards male or female chicks.

Statistical methods

Separate linear mixed models were run with a given estimate for chick development (growth rate, body mass and tarsus length) as the dependent variable and family treatment, chick sex and their interaction as categorical explanatory variables. Similar models were performed to test for behavioural differences (total begging intensity and parental feeding effort) between uniparental and biparental families on day 9. Family treatment, chick sex and their interaction were added to the model as explanatory variables. All models included original nest ID and foster nest ID as independent random factors to all models to adjust for a bias in statistical independence.

Results

Nestling development

A sexual dimorphism was observed in growth rate (male: $0.63 \pm 0.03$ g/day; female: $0.54 \pm 0.04$ g/day; $F_{1,36} = 3.74, P = 0.061$), body mass of fledglings (male: $17.4 \pm 0.4$ g; female: $16.0 \pm 0.5$ g; $F_{1,35} = 6.14, P = 0.018$) and at independence (male: $19.3 \pm 0.3$ g; female: $18.5 \pm 0.3$ g; $F_{1,26} = 3.67, P = 0.067$) and tarsus length (male: $18.0 \pm 0.1$ mm; female: $17.4 \pm 0.1$ mm; $F_{1,34} = 11.09, P = 0.002$). Overall, male fledglings were thus observed to be larger and heavier than females. The observed sex differences were consistent across family treatments for all the above parameters (treatment*chick sex interactions: all $P \geq 0.25$), except for tarsus
length for which a sexual size dimorphism tended to be more pronounced in uniparental families ($F_{1,34} = 3.94, P = 0.055$).

Chick begging and parental provisioning

Chick sex did not influence parental provisioning ($F_{1,35} = 0.12, P = 0.73$) or begging intensity ($F_{1,35} = 2.54, P = 0.12$) on day 9. Also across treatments, offspring sex had similar effects on both provisioning (interaction term: $F_{1,34} = 0.24, P = 0.63$) and begging ($F_{1,34} = 0.35, P = 0.56$) behaviour.
Table 1: Result of the mixed model explaining variation in parental provisioning rules

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Provisioning rules were investigated during the visibility manipulation experiment in biparental families. Explanatory variables include parental sex, visible and invisible type of manipulation, offspring begging intensity and chick mass prior to the video recording. Estimated effect sizes with SE are presented for the significant predictors. Only female estimates are given for sex-specific effects, as males are treated as the reference term and set at zero in the model output. The model accounts for genetic and environmental similarities among chicks (see Methods).
Figure legends:

**Figure 1:** Difference in (a) fledgling mass, (b) chick begging intensity and (c) parental feeding effort between uni- and biparental families on day 9. Mean ± 1 SE values are based on the parameter estimates of the statistical model.

**Figure 2:** Sexual difference in parental feeding effort during both temporary manipulations of split biparental families. Mean ± 1 SE values are based on the parameter estimates of the statistical model.
Figure 1:

(a) Fledging mass (g)

(b) Sqrt (Parental feeding effort)

(c) Sqrt (Begging intensity)

Family treatment

Biparental | Uniparental
Figure 2:

Visibility manipulation

Visible

Invisible

\[
\sqrt{\text{parental feeding effort}}
\]

Male parent
Female parent

Visibility manipulation