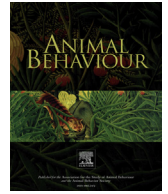




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Sex-specific negotiation rules in a costly conflict over parental care



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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.

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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 (Arnqvist, Edvardsson, Friberg, & Nilsson, 2000; Parker & Partridge, 1998), 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, Smiseth, & Kölliker, 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, Székely, & McNamara, 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 (Royle, Hartley, & Parker, 2006; Smith & Härdling, 2000). 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, Barta, Cuthill, & Székely, 2009).

The classic 'sealed bid' game-theoretical approach of Houston and Davies (1985) suggested that each parent benefits by exploiting its partner's effort until an evolutionarily stable level of care is

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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, Gasson, & Houston, 1999; McNamara, Houston, & Barta, 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, Houston, McNamara, & Székely, 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 (Lessells & McNamara, 2012; Royle, Hartley, & Parker, 2002, 2006). 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 (Hinde 2006; Johnstone & 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, Royle, & Hartley, 2002b; Smiseth, Wright, & Kölliker, 2008; Thorogood, Ewen, & Kilner, 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 (Hinde & Kilner, 2007; Houston et al., 2005).

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 (Harrison et al., 2009; Sasvári, 1986). 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, Kranenborg, & Tinbergen, 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 (Harrison et al., 2009; Johnstone & Hinde, 2006). 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 (50 × 64 cm and 40 cm high, GEHU cages, Nijverdal, The Netherlands) for territorial establishment and females were housed in one large internal aviary (2 × 2 × 2 m). 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 (Estramil, Eens, & Müller, 2013; Hinde, Buchanan, & Kilner,

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