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Consequences of biparental care for begging and growth in zebra finches, *Taeniopygia guttata*

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Although most (>90%) species of birds have biparental care, little is known about the consequences of such care for offspring behaviour and fitness-related traits. We examined the effect of biparental care on chick growth and begging behaviour in zebra finches, by comparing biparental broods with uniparental broods in which the male parent was removed and the brood size halved to control for potential parental workload. Differences in patterns of growth and begging behaviour between treatments therefore resulted from the difference in (1) the number of parents providing care and/or (2) the number of chicks per brood. Collaborating parents did not appear to act in concert and fed chicks independently of each other's feeding bouts. Broods reared by two parents were fed more frequently than those fed by one, and because biparental feeding bouts were less predictably spaced in time with less food available for each chick per feeding bout, competition was greater than in broods reared by single parents. Furthermore, chicks in biparental broods sustained an additional cost of begging: they had to beg almost twice as hard as chicks reared by single parents to receive a given amount of food, and they received less food per chick. Despite these effects, they grew faster. Growth rate may depend not just on the amount of food available but also on the frequency and predictability with which it is delivered, and, in particular, it reflects an adaptive response to competition for the available resources.

Biparental care is relatively rare in most taxa with parental care, but is common in birds (Clutton-Brock 1991). The main benefit of biparental care is an increase in the number of offspring that can be reared. However, although more offspring may be produced, sexual conflict between parents may lead to a reduction in offspring quality (Parker et al. 2002; Royle et al. 2002a; McNamara et al. 2003). Any decrease in parental investment as a result of sexual conflict will also result in increased conflict between parents and offspring and among siblings. Sexual conflict is consequently a key determinant of the overall level of intrafamilial conflict.

Intrafamilial conflict over parental investment increases with brood size, and family relationships become increasingly complicated if there is more than one sibling, as the parent has to choose which chick to feed. Each chick should 'value' itself more highly than any of its siblings, and so should compete to increase its share of available parental investment. Across bird species, the form of sibling competition varies from nonlethal 'scramble' competition to obligate siblicide, but in most cases the largest chicks within broods have a competitive advantage, gaining the biggest share of parental food input (Mock & Parker 1997). Since this competitive advantage increases with the size differential between chicks, sibling competition also puts a premium on rapid growth (Werschkul & Jackson 1979; Nilsson & Svensson 1996; Royle et al. 1999; Stockley & Parker 2002). However, although there are short-term competitive benefits to rapid growth, there are also potential long-term costs (Arendt 1997; Mangel & Stamps 2001; Metcalfe & Monaghan 2001), and there is little evidence that rapid growth per se increases fitness (Clarke 1998). Slower growth allows more of the available nutrients to be used in tissue maturation, maintenance and repair and in immunological defence (Ricklefs et al. 1998), and reduces oxidative stress

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(von Schantz et al. 1999). We should, therefore, expect to find trade-offs between rate of growth and offspring fitness, which are influenced by intrafamilial conflict.

Although most studies indicate that asymptotic size is highly heritable (van Noordwijk & Marks 1998), much of the variation in growth rate in birds is phenotypic and relates to variation in food availability (Schew & Ricklefs 1998). With altricial young, typically both parents feed and care for the offspring (biparental care). Since each parent would benefit if the other provided more care, sexual conflict can occur over parental investment (Trivers 1972). As a consequence of sexual conflict, zebra finch chicks reared by a single parent receive more parental investment than chicks reared by both parents when the potential workload per parent is held constant (Royle et al. 2002a). This result suggests that the main benefit of biparental care is an increase in the quantity but not the quality of offspring.

Theory suggests that, depending on the assumptions, a given-sized brood can fare better, equally or worse under biparental than uniparental care (McNamara et al. 2003), but few data are available on the consequences of biparental compared to uniparental care for offspring behaviour and fitness. Empirical work examining sexual conflict in biparental care has used two approaches. The first method is to handicap one parent, by cutting feathers or attaching small weights, to test the response of the nonhandicapped parent to a decrease in parental investment by the handicapped partner. Results vary from no response (e.g. Schwagmeyer et al. 2002), through partial compensatory response (less food is provided than to controls, but nonhandicapped individuals increase their provisioning; e.g. Markman et al. 1995) to full compensation (the brood receives as much food as controls do, as nonhandicapped partners make up the deficit in full; e.g. Wright & Cuthill 1990).

While these studies are informative with respect to the rules used by parents to determine relative parental investment rates and, hence, sexual conflict, they are less informative about the relative merits or otherwise of having two parents caring for young instead of one. To investigate this requires the removal of one caring parent from broods normally reared by two parents. Studies using this method have generally shown that single parents cannot successfully provision broods alone, as brood size is kept constant, which approximately doubles the potential workload (e.g. Bart & Tornes 1989; Markman et al. 1996). Consequently, although these studies show the importance of having two parents to rear 'normal' sized broods successfully (and the coevolution of biparental care with brood size; Smith & Härdling 2000), they tell us little about sexual conflict in biparental care and its consequences for offspring development and fitness. However, removal of a parent combined with a reduction in brood size to keep the potential workload constant offers a useful experimental design to examine the consequences for offspring of sexual conflict in biparental care. Case (1978) noted that in birds and mammals, species with biparental care have higher growth rates than uniparental species. Werschkul & Jackson (1979) suggested that when sibling competition is low, growth rates should also be slow. This general point was confirmed across species by Royle et al. (1999), using a comparative method. However, an unambiguous test of the effect of intrafamilial conflict on growth has not been considered within a species.

We experimentally examined the consequences of biparental care and sibling competition for chick growth and begging behaviour in zebra finches, a species with little or no sex differences in growth (Clotfelter 1996). We compared biparental broods (two parents and four chicks) with broods in which the male parent was removed and the brood size halved (uniparental; one parent and two chicks) to control for potential parental workload, using a crossover experimental design.

METHODS

Experimental Protocol

We used captive zebra finches from a variety of sources, including specialist breeders and stock from the University of Sheffield. Breeding females were paired with an arbitrarily selected, unrelated male in a breeding cage (120×45 cm and 40 cm high), with access to an externally attached nestbox (15 cm^3). Nestboxes were checked each morning and fresh eggs were marked and weighed (± 0.01 g). We randomly allocated 14 pairs of zebra finches equally to one of two groups once the clutch had hatched. Females in each group reared one brood of four chicks with the male and one brood of two chicks alone, thus keeping the potential parental workload constant in each regime. We reversed the order of the two regimes for the two groups. In group 1, the male was removed and brood size was maintained at, or reduced to, two when the chicks were 4–5 days old (chicks not required for the experiment were fostered to other broods as necessary). The female then reared these chicks alone until they reached independence at 35 days, when the young were removed to a separate cage. This was the 'uniparental care' regime. The male and female were then reunited and were allowed to start a second clutch. Both parents then reared the brood, which we adjusted as necessary so that the pair reared twice as many offspring (four) as the female had reared on her own (two). This was the 'biparental care' regime. In group 2 we reversed the order so that the biparental care regime preceded the uniparental care regime. Consequently, in both groups each female experienced both treatments (uni- and biparental care) consecutively, so that any effects of variation in parental investment on offspring fitness were not confounded by genetic differences between parents.

At hatching, chicks were individually marked with a nontoxic pen and then weighed each morning until 13–14 days old. Chicks were also weighed and measured (tarsus, wing and head–bill length ± 0.1 mm) at fledging (20 days), independence (35 days), and ages 50, 65 and 80 days.

Chicks reared under uniparental and biparental regimes were of similar age (mean of brood means $\pm$ SE: uniparental: 4.86 ± 0.79 days; biparental: 4.97 ± 0.83 days; paired t test: $t_{13} = 0.37$, $P = 0.71$) and mass (mean of brood