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Correspondence and requests for materials should be addressed to B.P.F. (e-mail: finney@ims.uaf.edu).

Sexual conflict reduces offspring fitness in zebra finches

Nick J. Royle*†, Ian R. Hartley* & Geoff A. Parker‡

* *School of Biological Sciences, IENS, University of Lancaster, Lancaster LA1 4YQ, UK*
‡ *Population & Evolutionary Biology Research Group, School of Biological Sciences, University of Liverpool, Liverpool L69 3GS, UK*

Parental care is often costly[1]; hence, in sexually reproducing species where both male and female parents rear their offspring (biparental care), sexual conflict over parental investment can arise[2]. Such conflict occurs because each care-giver would benefit from withholding parental investment for use with another partner, leading to a reduction in the amount of care given by one parent at the expense of the other[3–5]. Here we report experiments to explore the prediction from theory that parents rearing offspring alone may provide greater parental investment than when rearing offspring together with a partner[3,5]. We found that when the number of offspring per parent, and hence the potential workload, were kept constant, offspring received a greater per capita parental investment from single females than from both parents working together, and that males reared by single mothers were more sexually attractive as adults than their biparentally reared siblings. This difference between single- and two-parent families is due to a reduction in care provided by females when they care together with a male, rather than laziness by males or differences in the begging behaviour of chicks, supporting the claim that sexual conflict in biparental care can reduce the quality of offspring raised[3,5].

The importance of conflicts in evolutionary processes has been increasingly recognized in recent years[6–9]. In particular, sexual conflict over mating (pre-zygotic conflict) or parental investment (post-zygotic conflict) may be a powerful force shaping the potential for sexual selection[2,10], speciation[11] and the determination of life-history characteristics[12]. Although pre-zygotic sexual conflicts such as sperm competition are well characterized[13–17], there are very few demonstrations of the effects of post-zygotic sexual conflict on offspring fitness[18]. We used zebra finches (*Taeniopygia guttata*) to explore theoretical predictions from models of sexual conflict[3,5], which suggest that in some circumstances, single parents should provide greater parental investment per chick and at greater cost to themselves, compared with rearing chicks with a partner.

Fourteen pairs of zebra finches were allocated equally to one of two groups once clutches had hatched. Females in each group raised one brood of four chicks with the male, and one brood of two chicks alone, but the order in which this was done was different in the two groups. In group 1, the male was removed by replacing the cage partition and placing him in the half away from the nest and female (see Methods). Brood size was maintained at, or reduced to, two when the chicks were 4–5 days old, by which time chicks are able to self-thermoregulate. 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 re-united by the removal of the cage partition, and were allowed to start a second clutch. Both parents then reared the brood, which was adjusted as necessary so that the pair raised twice as many offspring (four) as the female had reared on her own (two). This was the 'biparental care' regime. In group 2, the order was reversed so that the biparental care regime preceded the uniparental care regime.

Consequently, in both of the groups each female experienced both treatments (uniparental and biparental care) consecutively, so that any effects of variation in parental investment on offspring fitness were not confounded by genetic effects. However, unlike previous male-removal experiments[19–23], which have generally shown that a single mother is unable to provide enough food for the full brood, we also simultaneously reduced brood size so that the number of chicks per parent remained constant. As the shape of the curve relating chick fitness to parental investment is likely to be set by the number of chicks per parent, any differences in parental

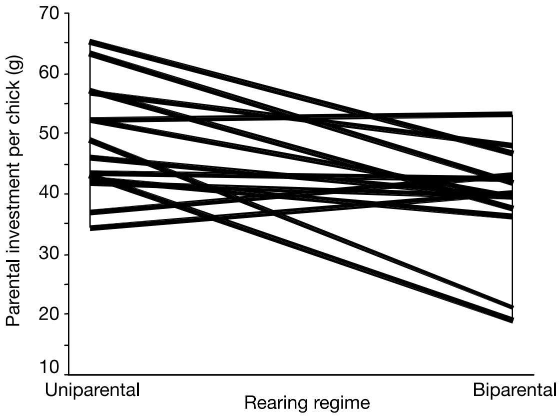

Figure 1 Parental investment for uniparental and biparental rearing regimes over a 15 day period after manipulation. Lines represent individual females. Our measure of parental investment, the amount of food consumed per chick, was greater under uniparental care (repeated measures general linear model, $F_{1,12} = 9.93$, $P = 0.008$).

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† Present address: Division of Environmental Biology, Graham Kerr Building, Glasgow University, Glasgow G12 8QQ, UK.

investment between uniparental and biparental regimes will be due to the effects of sexual conflict, rather than just being a consequence of a reduction in clutch or brood size (Box 1 reviews the current theoretical perspective).

Parental investment per chick (see Methods) on the day before experimental manipulation was similar in uniparental and biparental regimes (paired *t*-test, $t_{13} = 0.62$, $P = 0.55$). However, after manipulation, for the period between the start of the experiment and fledging, chicks raised under a uniparental regime received 25% more parental investment than their siblings raised by two parents (Fig. 1). The factor 'group' and its interaction with rearing regime were both nonsignificant ($P > 0.50$). As any difference in the predicted direction could be just a consequence of males working less hard whilst females maintain the same effort between treatments, it was necessary to assess relative male and female provisioning effort. Data from videos showed that males, rather than providing less parental investment, actually provide similar or greater amounts than females rearing chicks under a biparental regime. The number of feeds per hour was not different between male and female parents, or for females between uniparental versus biparental regimes ($P > 0.50$, paired *t*-tests), but the mean feed duration (load size) was greater in males than in females ($t_{11} = 2.38$, $P = 0.037$). In addition, females raising chicks under a uniparental regime also provided feeds of a greater size than when raising chicks under a biparental regime ($t_{11} = 2.34$, $P = 0.039$). This provided confirmation that females increased their workload when rearing broods alone.

As the definition in ref. 2 makes clear, the currency of parental investment is its cost in terms of the parent's ability to invest in other offspring. In the current experiment, the costs of reproduction were felt by parents of both sexes, although these were expressed in different ways. Males lost over 6% of their mass between pairing and brood independence when helping to rear broods under biparental care (paired *t*-test, $t_{13} = -2.97$, $P = 0.012$). In contrast, when separated from the female while she reared a brood alone, males increased their mass by 6% over the same period ($t_{13} = 2.25$, $P = 0.043$). Females did not change mass after biparental or uniparental regimes ($P = 0.17$ and 0.85, respectively; paired *t*-tests). Rather, investment in clutches (clutch mass) after a biparental care regime was over 20% greater than that after a uniparental regime (Fig. 2). This comprised an increase in both egg mass ($t_{13} = 2.50$, $P = 0.027$) and clutch size ($t_{13} = 3.31$, $P = 0.006$), and indicated greater parental investment by females raising broods alone.

The greater parental investment of single mothers had important consequences for offspring fitness. Chicks reared under biparental

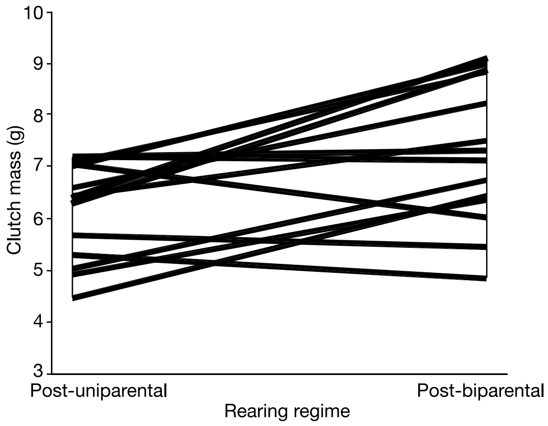

Figure 2 The mean mass of second clutches laid after the uniparental rearing regime (post-uniparental) is less than that of the biparental rearing regime (post-biparental; paired *t*-test, $t_{13} = 3.39$, $P = 0.005$). Lines represent individual females.

Box 1

Theoretical framework

Historical background

Smith and Fretwell[27] analysed optimal investment by a single parent with a fixed effort to expend on progeny. This approach was extended by ref. 3 assuming the fixed effort to be a fixed lifetime's parental investment, comparing evolutionarily stable strategy (ESS) investments of uniparental and biparental care species. Additional studies[25,28,29] examined ESS parental investment for species with biparental care, costing current expenditure in terms of lost future reproductive success. All of these approaches represent 'sealed bid' games: a parent is programmed to play a parental investment strategy independent of its mate's level of parental investment. Recently, ref. 30 modelled 'negotiation' games in which each parent responds in an ESS way to the current parental investment level of its mate, giving different ESS parental investment response levels from the 'sealed bid' approach.

Uniparental versus biparental care

Few theoretical analyses ask how offspring should fare when cared for by one parent rather than two. There are two obvious biological applications for this question, depending on whether parents are always either uniparental or always biparental (for example, comparison across species), or whether they face both situations during life, depending on circumstances (for example, uniparental care arising owing to mortality of a mate in a predominantly biparental species). One study[3] (see also ref. 24) concluded that in two otherwise equivalent species, one biparental and the other uniparental, where the parents are equal and where brood size does not affect the relation between an offspring's success and the parental investment it receives, offspring should fare worse in the biparental species because of sexual conflict. However, this solution, although an ESS, is not continuously stable[5], and this prediction cannot hold unless some modification can generate continuous stability. McNamara *et al.*[5] compared uniparental with biparental care, for a given brood size, in a single species. Most models (for example, ref. 29) result in more total parental investment being supplied under biparental care, although for a given parent, parental investment under uniparental care should be greater. This fits with many of the experimental manipulations in which one parent is removed[20]. However, certain cases (where parents are unequal, or there is negotiation) can result in less total parental investment in biparental situations.

Present experiment

The conclusions of ref. 5 relate to the case where a brood faces uniparental or biparental care, as could happen in nature. However, the instantaneous workload on a parent is greater if it must care for all the chicks on its own, rather than biparentally. Our experiments examine what happens when one parent rears two chicks singly, or shares equally with a partner the rearing of four chicks. The potential workload for a given parent is therefore equal in each situation. Note that in zebra finches, two and four are both naturally occurring brood sizes, and although parents are typically biparental, natural mortality is high, so that offspring are sometimes reared uniparentally. Conditions in the experiments can, therefore, be met in nature. Assuming that the behaviour we have observed is evolutionarily stable, this leaves two explanations for higher chick benefits under uniparental versus biparental care: parents are unequal and costs of parental investment are less for females, or conflict involves negotiation between parents, and the responsiveness of a given parent to a deficit by its mate is high. Although exact equality is unlikely, parental zebra finches are remarkably similar in their parental investment patterns. Furthermore, simple calculations (J. McNamara, personal communication) along 'sealed bid' lines suggest that if the costs of parental investment are less for the female, so that the two uniparental chicks fare better than the four biparental chicks, the female puts in more total effort with the four young than she does with the two (the male's effort is less than the female's and that is why the young fare worse with two parents). We found that females actually invest less in four chicks than in two, so the only explanation that seems compatible with our observations is that it represents the outcome of conflict between parents through negotiation.

and uniparental care regimes were of a similar size (head–bill, tarsus and wing length) and mass at all ages of measurement after fledging (all $P > 0.20$; paired *t*-test comparing brood means), but as adults, male chicks differed in their attractiveness to the opposite sex. In a mate choice experiment, the males raised under the uniparental care regime were more attractive to females than were their brothers raised under the biparental care regime (Fig. 3a). Additionally, of the 12 females used in the test, only three did not show an overall preference for males raised under the uniparental regime (Fig. 3b), and one of those (female 1) did not show any activity towards any male. Therefore, increased parental investment by females raising chicks under uniparental care regimes results in more attractive sons.

Manipulating brood size along with sexual conflict was important because we needed to control potential parental workload. We can, however, exclude the possibility that the difference in brood size between our treatment groups were the main influence on female parental investment, because nestling begging intensity over individual feeds did not differ between nests raised under uniparental compared to biparental regimes (N.J.R., I.R.H. and G.A.P., manuscript in preparation.). Additionally, smaller broods should provide a lower overall begging stimulus to parents[24], yet contrary to this prediction, broods of two chicks raised by single female zebra finches received more parental investment each than did chicks in broods of four raised by pairs.

Overall, this demonstrates that sexual conflict occurs when parents collaborate to rear young, and that parents are not entirely cooperative with one another[5]. In the conditions of our experiment, with equal potential parental workloads, full cooperation should result in equal expenditures under biparental and uniparental care. Current theory[5,25] predicts for our conditions that sexual conflict could result in either offspring faring equally, or offspring faring worse under biparental care (Box 1). The latter can occur if the cost of parental investment is asymmetric for the sexes[25], or if parents respond to the parental investment of the other parent by negotiation, and show high responsiveness to any deficit by the partner[5] (Box 1). Sexual conflict provides a clear cost to male offspring of a reduction in sexual attractiveness, and supports the view that biparental care can act to increase the number, but not the quality of offspring raised[3,5]. This provides empirical support that post-zygotic sexual conflict is an important determinant of the strength of sexual selection[2], and suggests that intra-familial conflicts may be as important in determining the characteristics of life-history traits, such as egg mass and clutch size[12], as are ecological variables, such as food supply. ☐

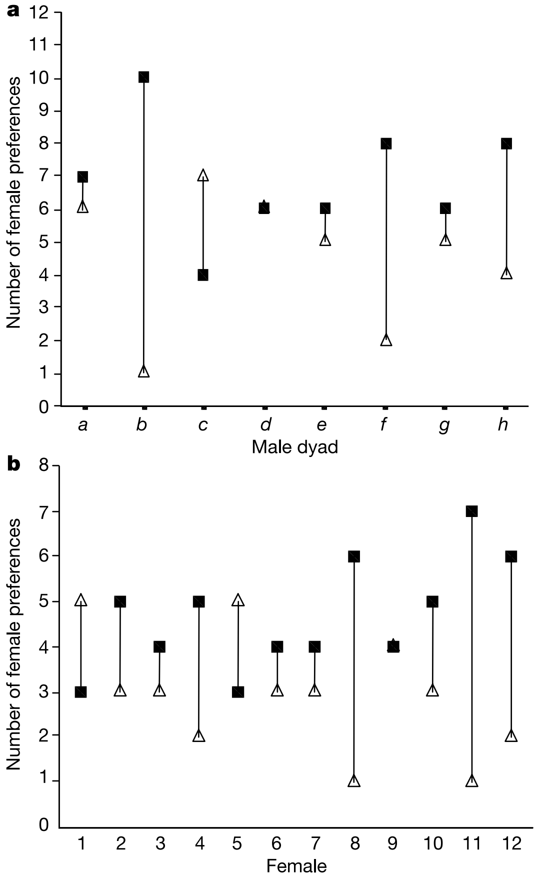

Figure 3 Mate choice experiment. **a**, Preference of females in relation to rearing regime for each male sibling-pair dyad (male dyads *a*–*h*). Females preferred males raised under the uniparental regime (Wilcoxon rank-sum test, $Z = 2.09$, $P = 0.037$). **b**, Preference of individual females in relation to rearing regime for male dyads. Again, females preferred males raised under the uniparental regime ($Z = 2.80$, $P = 0.005$). In **a** and **b**, uniparental-reared males are represented by filled squares, and biparental-reared males by triangles. Sample sizes may vary slightly between dyads owing to the loss of one female part of the way through the experiment.

Methods

Experimental protocol

Individual breeding females were put into one half of a partitioned breeding cage (120 × 45 × 40 cm), with access to an externally attached nest box. An arbitrarily selected, unrelated male was placed in the other half of the cage, but behind a partition so that neither bird could see the other. Before removal of the partition (pairing), we weighed (± 0.01 g) and measured (tarsus, wing and head–bill length ± 0.1 mm) birds. We checked nest boxes each morning, and we marked and weighed fresh eggs (± 0.01 g). At hatching, chicks were individually marked and then weighed each morning until 14 days of age. Chicks were also weighed and measured at fledging (20 days), independence (35 days), and at 50, 65 and 80 days of age. Where broods were supplemented by the addition of extra foster chicks from other nests, only original chicks (that is, full genetic siblings) were used for analyses of growth and reproduction. Unneeded offspring were fostered to other broods as necessary.

It was not always possible to have exactly four chicks in biparental-reared broods. Occasionally, broods reared one less or one more chick, but this was symmetrical with respect to group, and the overall mean was four chicks per brood. Parental investment per chick was independent of brood size, so that broods of three and five were indistinguishable from broods of four in the results. Chicks reared under uniparental and biparental regimes were of similar age (mean of brood means: uniparental, 4.86 ± 0.79 days; biparental, 4.97 ± 0.83 days) and mass (mean of brood means: uniparental, 4.02 ± 0.88 g; biparental, 3.99 ± 0.85 g) at manipulation (both $P > 0.70$; paired *t*-tests). Birds were freely provided with water, cuttlebone, grit, rearing food and seed daily (*ad libitum*), received a vitamin supplement and charcoal once a week, and were maintained throughout the experiment in a temperature-controlled room at 20 °C, under full spectrum, artificial light on a 16/8 h light/dark regime.

Measurement of parental investment

We established baseline feeding rates for each bird over 24 h periods for 3–4 days, by weighing seed provided and subtracting the weight of uneaten seed. Once paired, food consumption was measured daily for each pair. Parental investment was calculated, on a daily basis, as the amount of food consumed minus the parent's baseline, which was assumed to remain constant throughout the chick-rearing period. Unless otherwise stated, parental investment is expressed as the amount of parental investment per chick.

Parental provisioning effort and chick-begging behaviour were assessed using video cameras recording through a hole in the front of each nest box, which was covered when not recording. We acclimatized birds to the camera and tripod over a 24 h period before recording. However, at two nests, either one or both of the parents did not feed young during the recording session (but immediately fed the young once the camera was removed), so the sample size for analysis was 12 pairs. We measured the mass of food before and after the 3 h video recording. Chicks were weighed and individually marked before video recording, using correcting fluid, and the amount of food in each chick's crop was scored on a five-point scale (0 being empty and four being full). The total number of feeds in 3 h and the mean regurgitate duration (feed load size) for the first five feeds from each hour of video (fifteen feeds in total) were calculated for parents at all nests. Parents were scored as having fed a chick when they inserted their bill into the chick's gaping mouth and they could be seen regurgitating, with characteristic heaves of their bodies. Regurgitate duration was measured frame by frame, from the point at which parents inserted their bill until it was withdrawn from the chick's mouth.

Mate choice experiment

Twelve experienced females (all had reared at least two broods) were introduced sequentially for 10 min periods into a bi-directional mate choice cage, which had a wire mesh partition at either end, each of which was connected to a cage containing a test male. Birds could therefore see each other, but could not make physical contact. Two perches were mounted in the female compartment, which were equidistant from the cages at either end that separately housed the two males. Test males were 'dyads' of sibling males from uni- and biparentally reared broods. Male dyads, therefore, had the same genetic parents, and the only difference between them was that one was raised under a uniparental regime and the other a biparental regime. Males had fresh food and water available throughout the experiment. Before being introduced to the mate choice apparatus, females were housed in a cage out of sight of the test males, so were unable to assess the choice of other females or make any previous assessment of either male. The order in which females were introduced to males was varied between each sibling pair. Trials were video-recorded by N.J.R. and watched by I.R.H., who was unaware of the identity of the test males. Females were recorded as making a preference for the male on the side of the cage at which she spent most of her time during the test. The experiment was conducted under the required conditions of ultraviolet (full spectrum) lighting[26].

Statistical analysis

We analysed the data using SPSS for Windows 10.0 and S-Plus 2000. We tested all data for normality and homogeneity of variances before analysis. All tests are two-tailed.

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Correspondence and requests for materials should be addressed to I.R.H.
(e-mail: i.hartley@lancaster.ac.uk).

Direct cortical input modulates plasticity and spiking in CA1 pyramidal neurons

Miguel Remondes & Erin M. Schuman

Caltech/Howard Hughes Medical Institute, Division of Biology, 216-76, Pasadena, California 91125, USA

The hippocampus is necessary for the acquisition and retrieval of declarative memories[1,2]. The best-characterized sensory input to the hippocampus is the perforant path projection from layer II of entorhinal cortex (EC) to the dentate gyrus[3,4]. Signals are then processed sequentially in the hippocampal CA fields before returning to the cortex via CA1 pyramidal neuron spikes. There is another EC input—the temporoammonic (TA) pathway—consisting of axons from layer III EC neurons that make synaptic contacts on the distal dendrites of CA1 neurons[3,5,6]. Here we show that this pathway modulates both the plasticity and the output of the rat hippocampal formation. Bursts of TA activity can, depending on their timing, either increase or decrease the probability of Schaffer-collateral (SC)-evoked CA1 spikes. TA bursts can also significantly reduce the magnitude of synaptic potentiation at SC–CA1 synapses. The TA–CA1 synapse itself exhibits both long-term depression (LTD) and long-term potentiation (LTP). This capacity for bi-directional plasticity can, in turn, regulate the TA modulation of CA1 activity: LTP or LTD of the TA pathway either enhances or diminishes the gating of CA1 spikes and plasticity inhibition, respectively.

Using hippocampal slices optimized for stimulating both the SC and TA inputs[7,8] (Fig. 1a, b), we examined whether TA activity can gate SC-elicited spikes in CA1 pyramidal neurons. We first began with an SC stimulus strength that consistently evoked an excitatory postsynaptic potential (EPSP) but never a spike (Fig. 1c). We found that when the SC stimulus was immediately preceded by a TA burst (10 stimuli at 100 Hz), the previously ineffective SC stimulus now evoked a spike. The spike enhancement occurred when the TA stimulus preceded the SC stimulus by 20–80 ms, suggesting temporal summation of the TA- and SC-elicited EPSPs (Fig. 1c, d). The opposite phenomenon, spike-blocking[8,9], can also be observed. In this case, the SC axons are stimulated at a strength that reliably elicits a CA1 spike. If a short burst is delivered to TA axons about 400 ms before the SC stimulus, SC-elicited spiking of CA1 neurons is prevented (Fig. 1e). This is due to a GABA_B (γ-aminobutyric acid)-mediated IPSP that reduces postsynaptic excitability; this IPSP can last for up to 1 s after a TA burst[8]. These data show that, depending on the relative timing of the TA input and the strength of SC stimulation, TA activity can either facilitate or block CA1 output. When a burst of TA activity precedes SC activity by $\leq$100 ms, SC-elicited spiking will tend to be facilitated. Conversely, TA activity that precedes SC activity by as much as 200 ms will tend to inhibit SC-elicited spiking. Because CA1 neuron activity constitutes the principal output of the hippocampal formation, these data suggest that TA activity can gate information transfer out of the hippocampus.

The capacity for TA activation to influence SC-driven spiking suggests that TA activity might also modulate plasticity at the SC–CA synapses. Indeed an earlier study indicated that stimulation of the TA pathway could reduce LTP at the SC–CA1 synapses[10]. We re-examined this issue in the following way: we first determined a SC theta burst stimulation (TBS) protocol that could be applied repeatedly, each time yielding roughly the same magnitude and pattern of synaptic potentiation (Fig. 2a, d). We then examined the