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Parent–offspring conflict and motivational control of brooding in an amphipod (Crustacea)

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Models of parent–offspring conflict concerning levels of caregiving centre on conflict resolution by offspring control, compromise or offspring 'honest signalling' that parents use to maximize their own fitness. Recent empirical studies on motivational control of parental feeding of offspring are interpreted as supporting the latter model. Here, we examine parental care in an amphipod, *Crangonyx pseudogracilis*, which directs care to embryos in a brood pouch. Embryo removal and transplantation elucidated causal factors that determine levels of caregiving. In the short-term, females with all embryos removed reduced care activities, but partial embryo removal did not affect caregiving, evidence of 'unshared' parental care. In the long-term, females with all embryos removed ceased care. Thus, females have a maternal state that is maintained by stimuli from offspring. Transplantation of early/late stage embryos among females originally carrying early/late stage embryos revealed that stimuli from embryos indicate their age-dependent needs, but only modify caregiving within the constraints of a changing endogenous maternal state. Thus, we demonstrate that mothers and offspring share motivational control of care. However, we highlight the inappropriate use of motivational data in reaching conclusions about the resolution of parent–offspring conflict.

Keywords: parent–offspring conflict; maternal care; motivational control; amphipod

1. INTRODUCTION

There is inherent asymmetry in the costs and benefits of giving and receiving parental care, since the cost of receiving care to any one offspring is reduced ability of the parent to invest in future (or other current) siblings, to which the offspring is related by 0.5 (in a monogamous species) or 0.25 (in a non-monogamous species). But the benefit of receiving that care is the enhanced survival of all that offspring's genotype (Trivers 1974). Thus, there will be occasions when a parent would maximize its fitness by not giving additional care to the existing offspring, whereas it would enhance the inclusive fitness (Hamilton 1964) of the offspring by receiving that additional care. The result is parent–offspring conflict, the latter demanding (signalling) for more care than would maximize fitness of the former (Trivers 1974). This conflict would apply to how much care to give on any one day or when to stop care such that the young become independent (Trivers 1974).

This realization spawned numerous theoretical studies examining the resolution of conflict (see Godfray & Johnstone 2000; Parker *et al.* 2002). At one extreme, offspring have control, their gain in parental investment being matched to their signalling effort and care obtained according to the offspring's interest. At the other extreme is parental control, whereby the parent monitors signals from the young, which are costly and honest, but care is allocated according to parental interests (Godfray 1991, 1995). Between these extremes are compromise models, in which mother and offspring each achieve their fitness interests partially (Parker & MacNair 1979).

Experimentally distinguishing between these models is difficult (Godfray & Johnstone 2000; Parker *et al.* 2002). Studies that demonstrate parental responsiveness to offspring begging for food in birds, mammals (Kilner 1995; Kilner & Johnstone 1997) and invertebrates (Rauter & Moore 1999) are interpreted as supporting honest signalling and parental control. However, simply demonstrating responsiveness of parents to offspring signals does not distinguish between honest signal models and shared or offspring control. Here, we employ embryo removals and cross-fostering in an amphipod that shows active maternal care in order to elucidate factors involved in the determination of levels of maternal care and consider implications for conflict resolution.

Female amphipods extrude eggs into a brood pouch, where they are fertilized, develop and hatch. The freshwater *Crangonyx pseudogracilis* and marine *Ahperusa jurinei* provide active care of developing embryos, engaging in bouts of curling and stretching (Dick *et al.* 1998, 2002; see also Tarutis *et al.* 2005). This results in the ejection of non-viable/dead embryos, ventilation of the brood pouch and cycling of the embryos. Low oxygen increases this activity (Dick *et al.* 1998, 2002; Tarutis *et al.* 2005). In *C. pseudogracilis*, the level of care is high during early embryo development, thereafter declining and stops when the young naturally leave the brood pouch (*ca* 10 days after extrusion at 20 °C; Sutcliffe & Carrick 1981; Dick *et al.* 1998). We assume that both embryos and mother benefit in fitness terms from the higher level of brooding given to the younger as compared to older broods. But we do not know the precise level that would maximize the fitness of one player at the expense of the other. We also assume that brooding is costly in females (see Fernández *et al.* 2000). In *A. jurinei*, we showed by embryo removals that brooding level is a function of both female 'maternal state' and stimuli from offspring (Dick *et al.* 2002). In the present study, using *C. pseudogracilis* (see also Dick *et al.* 1998), we comprehensively examined the interplay between the changing 'maternal state' of mothers (over time since egg extrusion), and the actual developmental stages of embryos, by combining embryo removals with embryo cross-fostering transplantation experiments.

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2. MATERIAL AND METHODS

(a) *Experiment 1: short-term response to partial and total embryo removal*

Crangonyx pseudogracilis were collected from Kiltonga Lake, Co. Down, Northern Ireland (Grid Ref. J477746) in July/August 1998 and housed in aquaria with lake water at 20 °C and flora and fauna (principally *Elodea canadensis*, detritus and *Asellus aquaticus*). The day following collection, females with embryos were subjected to experimental manipulation. Throughout, females were chosen on the basis of having, on visual inspection, well-filled brood pouches. We excluded females with few embryos and with excessive numbers of embryos (one female with 98 embryos had difficulty in moving!). We established here that mean embryo number was 22 and range 16–32. In this first experiment, females with early stage embryos (stage 1; approx. 1–3 days from extrusion, see Sutcliffe & Carrick 1981; Dick *et al.* 1998) were randomly assigned to four experimental groups ($n=20$ each): (i) normal, without manipulation; (ii) sham, where embryos were disturbed within the brood pouch for 2 min with a pipette; (iii) 50% embryos removed with the pipette; and (iv) 100% removed. In all the experiments, total time in brood care activities (time spent curling plus stretching) was recorded for 15 min for each female in crystallizing dishes, 9 cm diameter, 3 cm depth filtered lake water at 20 °C, oxygen content 5 mg l^{-1} (55% saturation). Females were maintained in their individual dishes and oxygen monitored with a Jenway O_2 meter, aeration to maintain oxygen levels being given where required by mixing the water whilst bubbling air through an air stone. In this experiment, brood care was recorded at 12 h post-operation. The data for all experiments were $\log_{10}$ transformed and for this experiment subjected to a one-factor ANOVA with the Fisher's protected least significant difference *post hoc* test (FPLSD).

(b) *Experiment 2: long-term response to embryo removal*

Females with early stage embryos (stage 1) were assigned to two experimental groups ($n=20$ each): (i) sham; and (ii) 100% removed. Brood care was recorded at 24, 48 and 72 h post-operation and analysed by two-factor ANOVA (time as repeated measure).

(c) *Experiment 3: response to embryo transplants*

Females with early (stage 1) and late stage embryos (stage 4, 7–8 days from extrusion) had all embryos removed and were given either early or late stage embryos from another female (i.e. 2×2 factorial design, $n=20$ each group) and analysed by two-factor ANOVA. Each female received eight embryos delivered into the brood pouch by pipette. Brood care was recorded at 24 h post-operation.

3. RESULTS

(a) *Experiment 1: short-term response to partial and total embryo removal*

There was a significant difference in the levels of brood care among the four experimental groups ($F_{3,76}=27.5$, $p<0.001$). However, there was no significant difference among normal, sham operated or females with 50% of their brood removed (FPLSD). Only females with 100% brood removal showed significantly reduced brooding (different from all others at $p<0.001$; FPLSD), exhibiting around 75% of normal brooding times.

(b) *Experiment 2: long-term response to embryo removal*

There was an overall decline in maternal brooding (figure 1) with time post-removal of embryos (repeated measure effect $F_{2,40}=56.8$, $p<0.001$) and an overall reduction when the embryos were removed ($F_{1,40}=401.7$, $p<0.001$). There was a significant interaction effect ($F_{2,40}=68.6$, $p<0.001$), because there was no change in brooding by sham-operated females over 72 h, but those with 100% embryos removed showed a decline to zero (figure 1).

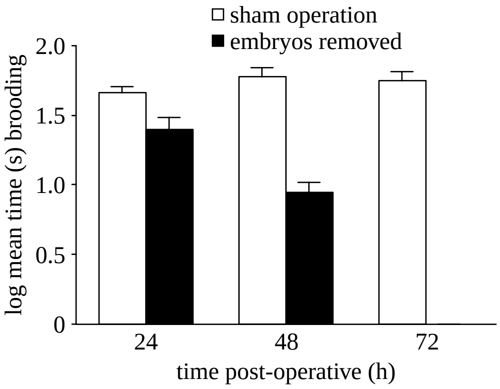

Figure 1. Decline in maternal care with time post-removal of embryos. $\log_{10}$ mean (+s.e.) total time in brood care activities in 15 min is shown.

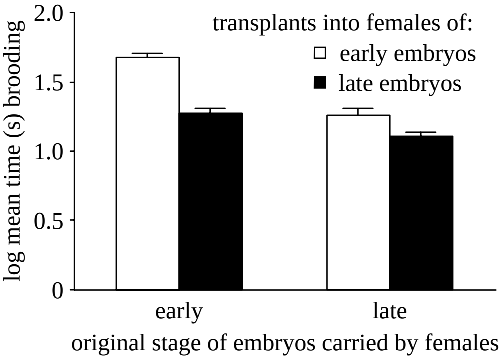

Figure 2. Brooding by females originally with early or late stage embryos when early or late stage embryos were transplanted into brood pouches. $\log_{10}$ mean (+s.e.) total time in brood care activities in 15 min is shown.

(c) *Experiment 3: response to embryo transplants*

Brooding by late stage females was significantly lower (figure 2) than early stage females ($F_{1,28}=65.2$, $p<0.0001$) and females with transplanted late stage embryos exhibited significantly less brood care than the early stage transplants ($F_{1,28}=59.1$, $p<0.001$). There was a significant interaction effect ($F_{1,28}=11.3$, $p<0.001$), because the effect of embryo stage was less marked with late stage females than with early stage females (figure 2). All the groups differ from each other ($p<0.005$; FPLSD) except early females with late embryos versus late females with early embryos.

4. DISCUSSION

Females with 50% of their embryos (early stage) removed continued to brood normally at 12 h post-removal, and did not differ from sham-operated or unmanipulated females; only females with 100% embryos removed showed a significant decline in brooding (see also Dick *et al.* 2002). Thus, complete embryo absence, but not reduced numbers, reduces brooding levels. Females increase care when ambient dissolved oxygen levels decrease (Dick *et al.* 1998, 2002), indicating that ventilation is a key function of care. However, there was no reduction in care with

50% embryo removal, even though the reduced brood would use less oxygen. Furthermore, in experiment 3, we cross-fostered eight embryos into each female, a marked reduction from the mean of 22, and yet brooding appeared normal when the brood age was appropriate for female stage. Thus, brooding appears to be uninfluenced by brood size and hence not by oxygen depletion within the brood pouch, although we need to measure oxygen levels in the brood pouch to confirm this. It could be argued that maternal use of oxygen is constant regardless of embryo numbers and this explains constancy in the expression of behaviour associated with oxygen provision. However, since females continually ventilate their gills with pleopod beating, whether brooding or not, and these gills are outside the brood pouch, this seems unlikely. In any event, independence of brood care levels from brood size is consistent with the concept of 'unshared' parental investment (i.e. activity can equally benefit more than one offspring, such as warning calls; Lazarus & Inglis 1986), as opposed to the 'shared' parental investment (i.e. activity is distributed among offspring, such as food provision; Lazarus & Inglis 1986) noted in the parental feeding of birds (Kilner 1995; Kilner & Johnstone 1997) and larvae of beetles (Rauter & Moore 1999).

Although females with all embryos (early stage) removed continued to brood at 24 and 48 h post-operation, albeit at significantly lower levels than sham-operated females, brooding ceased by 72 h. This slow decline in brooding when all the embryos were removed, rather than immediate cessation, indicates a degree of internal control of maternal care, i.e. a maternal state. However, the eventual cessation indicates that stimuli from the embryos maintain or enhance this maternal state.

In experiment 3, we examined care after embryo cross-fostering by transplantation. This showed a significant effect of embryo stage, thus demonstrating maternal responsiveness to exogenous, age-dependent stimuli from the young. There was also an effect of female stage, demonstrating that females moderate responses to these stimuli according to the developmental stage of their original brood. Early stage females also appeared more discriminating between embryo stages than late stage females.

For females to respond to offspring developmental stage, the offspring must provide stimuli that indicate need appropriate to age. However, the maternal response is markedly influenced by the female reproductive stage and hence expectation of true offspring need. One might argue that this suggests compromise, as it seems that the female is only partially responsive to offspring stimuli. However, without knowing the optimal behavioural strategy for each, it is not possible to determine the precise extent to which the mother or offspring maximize their own fitness under normal conditions. Thus, the data fit the model of honest signalling and parental control of fitness consequences (Godfray 1991, 1995; Parker *et al.* 2002) and also of shared control, i.e. compromise on fitness consequences (Parker & MacNair 1979). Total offspring control in terms of fitness consequences (Parker *et al.* 2002) seems unlikely because of their immature state. However, that too cannot be excluded by the present data. What we have shown is that both the developmental stage of the embryos and the maternal stage of the female are causal factors in the motivational control (*sensu* Sibley & McFarland 1974) of maternal care. Demonstration of the nature of motivational control, however, cannot be interpreted as a clear guide to fitness consequences or resolution of parent–offspring conflict in this or other empirical studies, such as those on birds (e.g. Kilner 1995) and invertebrates (e.g. Rauter & Moore 1999).

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