The asymmetric incubation game: a prospective model and a house sparrow investigation

G. A. Parker [a],[*], P. L. Schwagmeyer [b], Douglas W. Mock [b]

[a] Department of Evolution, Ecology and Behaviour, Institute of Integrative Biology, University of Liverpool, U.K.
[b] Department of Biology, University of Oklahoma, Norman, U.S.A.

Many birds show biparental incubation patterns in which male and female parents alternate their incubation bouts. We constructed prospective sealed bid (rather than negotiation) models of optimal (both cooperative and ESS) incubation bout lengths for each sex ('the incubation game') to examine whether the asymmetry in incubation efficiency can generate sex biases in incubation bout lengths. This model may apply generally when two individuals cooperate in alternating bouts to complete a task requiring a fixed total effort, but where one individual accomplishes more per unit time spent on the task than the other, and where bout lengths can be varied strategically. Both the cooperative (suitable for true monogamy) and the (more realistic) ESS versions predict that the less efficient partner should perform shorter bouts, although the ESS model predicts that both partners should perform shorter bouts than the cooperative model. We explored these predictions with field data on house sparrow, *Passer domesticus*, incubation. Previous work has shown that male bouts are typically shorter than female bouts. Here, we tested the model's prediction that such an asymmetry in parental care may result from differences in the relative competence of each sex at transferring heat during incubation. Females were notably more efficient incubators: they warmed the nest more than males during the first 4 min of their bouts, increased mean nest temperatures more per degree starting temperature and, by the end of their bouts, they had elevated both final nest temperature and mean nest temperature more per minute than males. Thus, even in the absence of sex differences in parentage, asymmetries in parental effectiveness can promote disparities between the sexes in cooperative investment. We discuss the implications for sexual conflict of parental asymmetries in the value of care.

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Biparental care, common in birds, generates sexual conflict over the extent of care from each parent unless there is true monogamy (i.e. where two parents can produce progeny only with each other; Mock & Parker, 1997). Theoretical considerations of sexual asymmetries in the costs or benefits of parental care have provided important insights into the evolution of species differences in parental care patterns. By far the most commonly addressed asymmetries stem from potential sex differences in parentage (i.e. the proportion of offspring in the clutch that derive from the caring male relative to the caring female). Lower parentage in the male through extrapair fertilizations (EPFs) can be viewed as reducing the benefit to males of providing care, and/or as imposing an opportunity cost of male care (e.g., Houston & McNamara, 2002; Kokko, 1999; Maynard Smith, 1978; Parker, 1985; Queller, 1997; Westneat & Sherman, 1993; Yamamura & Tsuji, 1993).

Our focus here concerns a different asymmetry, namely a situation in which male and female parents are not equally effective at parental care. Sexual asymmetries in the value of care to offspring have often been considered in the context of discrete strategy games, wherein parents either provide care or desert the brood; a parent's decision to desert is predicted to depend on many variables including those associated with asymmetries between itself and its mate in energy reserves, parentage, parental foraging efficiency, etc. (Barta, Houston, McNamara, & Szekely, 2002; McNamara, Székely, Webb, & Houston, 2000). Compared to asymmetries in parentage, however, theoretical treatments of the effects of sexual asymmetries in the value of care to offspring have been relatively neglected, perhaps because empirical work on biparental care has often focused on tasks at which the sexes are likely to be equally good. A notable exception has been research on role specialization associated with size-based asymmetries in parental competence at territory defence (e.g. Itzkowitz, Santangelo,

* Correspondence: G. A. Parker, Department of Evolution, Ecology and Behaviour, Institute of Integrative Biology, University of Liverpool, L69 7ZB, U.K.
Tel.: +44 0151 336 4202.
E-mail address: gap@liv.ac.uk (G. A. Parker).

Cleveland, Bockelman, & Richter, 2005) or foraging behaviour (e.g. Weimerskirch et al., 2009). Recently, though, studies comparing the effectiveness of avian male versus female contributions to incubation have revealed not only the existence of asymmetries in some species, but also variation among species in which sex is more effective (Auer, Bassar, & Martin, 2007; cf. Reid, Monaghan, & Ruxton, 2002; Voss, Rutter, Zimmerman, & Moll, 2008).

Incubation as a specific aspect of biparental care has attracted little theoretical attention. Jones, Ruxton, and Monaghan (2002) adopted a graphical approach to examine the case where incubation has an increasing mortality cost for each parent (depending on its condition), which determines when a parent reaches an 'abandonment threshold'. They assumed full compensation between parents, and discussed the implications for sexual conflict. In the present paper we investigate a simple theoretical model ('the incubation game') involving alternating incubation bouts between male and female parents. A fixed amount of incubation is required to complete development to hatching. Each parent can vary how long it incubates at each bout, and we specifically consider the potential impact of sexual asymmetries in incubation effectiveness on incubation bout lengths. We examine three versions of this model. The first version examines the optimal bout length for a single parent, the second is a cooperative game between two parents that maximizes the pair's reproductive output (appropriate if the pair mate for life; i.e. 'true monogamy' sensu Mock and Parker, 1997), and the third seeks a noncooperative evolutionarily stable strategy (ESS; Maynard Smith, 1982) solution (appropriate if successive new partners can be found without cost). We then provide empirical evidence from a study of house sparrows, *Passer domesticus*, that the difference in incubation bout lengths in males and females (Schwagmeyer, Bartlett, & Schwabl, 2008) is associated with a difference in their relative competence at rewarming and maintaining nest temperatures during incubation, as predicted by our biparental care models. The incubation game has general significance; it may apply to cases where two individuals cooperate in alternating bouts to complete a task requiring a fixed total effort, but where each inputs effort at different rates to the task. Finally, we discuss the implications of asymmetries in the value of care for sexual conflict: whereas asymmetries in parentage typically unilaterally affect the fitness gain of males, asymmetries in the value of care to offspring affect the fitness of both parents.

THE INCUBATION GAME

Our approach is prospective only, and not intended for biological precision; we seek simply to determine qualitatively the probable evolutionary responses to parental asymmetries in incubation efficiency.

Optimal Incubation Bout Length for a Single Parent

Suppose that only one parent (say, the female) incubates. She has a strategic 'choice' (i.e. through selection) of time, t_{iF} to spend in each bout of n successive incubation bouts before hatching occurs. The total incubation requirement I (which can be regarded as a number of thermal incubation units needed to allow development to hatching, e.g. Gillooly, Charnov, West, Savage, & Brown, 2002) is supplied at a rate (for the female) α_F in each time unit of incubation. Thus α is a measure of the parent's 'incubation efficiency'; the higher the value of α, the faster that embryonic development occurs.

For simplicity, development is assumed to occur only during incubation (not during time spent away from the nest by the female). While some development may occur during the time spent

away from the nest, provided that this is small compared to development during incubation, it should not significantly affect the predictions. The number of incubation bouts required for eggs to develop to hatching is given by

$$n(t_{iF}) = I/(\alpha_F t_{iF}). \tag{1}$$

We make three simple assumptions in order to find an optimal incubation bout length. (1) The costs of incubating, $C(t_{iF})$, a measure of the probability of loss in future broods as a result of each incubation bout length t_{iF}, increase at an accelerating rate during each incubation bout. (2) After an incubation bout, the female leaves the nest in order to perform maintenance activities such as feeding; costs $C(t_{iF})$ begin to accumulate again when she returns for the next incubation bout (with $t_{iF} = 0$ at the start of each incubation bout). (3) There is additionally some cost (such as a risk of nest mortality; costs of cooling) incurred each time the nest is left by the female (see below). We model these costs of leaving the nest as a probability, $S(n)$, that the nest survives, which is a declining function of n, and hence in view of (1), an increasing function of t_{iF}.

Thus the fitness of the single female parent is

$$W_F(t_{iF}) = S(n) - nC_F(t_{iF}). \tag{2}$$

Note that the costs, $C(t_{iF})$, are those that accumulate throughout the entire incubation period, and do not include temporary costs recovered during intervals of foraging or resting between incubation bouts (e.g. Williams, 1996 found net daily energy deficits in incubating adults). Differentiating $W_F(t_{iF})$ with respect to t_{iF}^* and setting to zero we obtain the general equation

$$S'(n(t_{iF}))n'(t_{iF}) - n'(t_{iF})C(t_{iF}) - n(t_{iF})C'(t_{iF}) = 0,$$

and substituting the form for $n(t_{iF})$ in equation (1), we obtain the optimal bout length, t_{iF}^*, subject to $d^2 t_{iF}/dt_{iF}^2 < 0$ for a maximum, as

$$C_F'\left(t_{iF}^*\right) = \left[-S'\left(n^*\right) + C_F\left(t_{iF}^*\right)\right]/t_{iF}^*, \tag{3}$$

where the primes indicate the differential coefficient of the function with respect to the variable specified (e.g. $C_F'(t_{iF}^*) = dC_F/dt_{iF}$ at t_{iF}^*). Note that for the single parent, the term α_F occurs only implicitly in the term $n^* = I/(\alpha_F t_{iF}^*)$.

A Cooperative Solution for Optimal Bout Lengths with Biparental Care

We next investigate biparental care with 'true monogamy' (sensu Parker, 1985; Mock & Parker, 1997), that is, where parents remain monogamous and cannot mate with an alternative partner should the first partner die. The fitness interests of the two parents are thus entirely congruent; there exists no sexual conflict (sensu Parker 1979). While few (if any) species show true monogamy, many socially monogamous birds suffer severe constraints on future reproduction after the loss of a mate, such that costs to a mate's future reproduction may be at least partially experienced by its partner.

Each parent can now independently vary his/her time spent per incubation bout, i.e. t_{iF} for the female, t_{iM} for the male. The rules of the game remain essentially similar as for the single parent, but one partner forages while the other incubates. Thus we assume that there is an evolved convention that incubation bouts alternate between male and female: a female incubation bout is followed (either immediately or some time after the female leaves the nest) by a male incubation bout, and vice versa. Since parents are constrained by true monogamy, selection favours the cooperative solution for the pair of bout lengths (t_{iF}^*, t_{iM}^*) that maximizes the