LUND UNIVERSITY

Clutch size evolution under sexual conflict enhances the stability of mating systems

Smith, Henrik; Härdling, Roger

Link to publication

Clutch size evolution under sexual conflict enhances the stability of mating systems

Henrik G. Smith[1][*] and Roger Härdling[2]

[1]*Department of Animal Ecology, and* [2]*Department of Theoretical Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden*

Models of optimal clutch size often implicitly assume a situation with uniparental care. However, the evolutionary conflict between males and females over the division of parental care will have a major influence on the evolution of clutch size. Since clutch size is a female trait, a male has little possibility of directly influencing it. However, the optimal clutch size from a female's perspective will depend on the amount of paternal care her mate is expected to provide. The sexual conflict over parental care will in its turn be affected by clutch size, since a larger clutch makes male care more valuable. Hence, there will be joint evolution of mating system and clutch size. In this paper, we demonstrate that this joint evolution will tend to stabilize the mating system. In a situation with conventional sex roles, this joint evolution might result in either increased clutch size and biparental care or reduced clutch size and uniparental female care. Under some circumstances the initial conditions might determine which will be the outcome. These results demonstrate that it may be difficult to deduce whether biparental care evolved because of few opportunities for breeding males increasing their fitness by attracting additional mates or because of the importance of male care for offspring fitness by studying prevailing mating systems using, for example, male removals or manipulation of males' opportunities for finding additional mates. In general terms, we demonstrate that models of life-history evolution have to consider the social context in which they evolve.

Keywords: life-history strategies; clutch size; mating system; paternal care; evolutionary stable strategy

1. INTRODUCTION

Evolution of clutch size is a central theme in life-history theory (Roff 1992; Stearns 1992). In an early formulation, Lack (1947) suggested that a female should produce the clutch size that results in the maximum number of surviving young, thus acknowledging the fact that an increased clutch size will result in less investment per offspring. Williams (1966) suggested that parents also trade current against future reproduction and that the optimal clutch size is the one which maximizes lifetime reproductive success. However, these and other models of optimal clutch size implicitly assume a situation with uniparental care (Godfray & Parker 1991).

Whenever more than one parent provides parental care there will be sexual conflict over the amount and division of care (Trivers 1972). First, there will be a conflict over the division of parental care because it will pay one parent to reduce its investment if it can thereby 'persuade' the other parent to increase its investment (Chase 1980; Houston & Davies 1985). Second, there may be sexual conflict over the amount of care that should be given because males and females do not value current and future reproduction in the same way. For example, in animals with internal fertilization social and genetic motherhood are often identical, whereas a social father may not always be certain that he is also the genetic father (Westneat *et al.* 1990). Reproduction may also affect future fecundity differently in males and females because males' fitness is often more limited by the availability of mates than that of females (Trivers 1972). For example, males typically have greater opportunities for increasing their fitness through extra-pair copulations

(Westneat *et al.* 1990) or by attracting additional mates (Emlen & Oring 1977) and may therefore pay a higher opportunity cost in terms of lost fitness by providing care. Some studies have directly demonstrated that use of time and energy for paternal care and mate attraction (Whittingham 1993; Cucco & Malacarne 1997) or paternal care and mate guarding of additional females (Hasselquist & Bensch 1991; Whittingham 1994) may be in conflict. The costs and benefits of parental care will determine whether either or both parents care or not (Maynard Smith 1977) and, in a situation with biparental care, there may be an evolutionary stable division of labour. A stable division of labour will depend on sexual differences in the costs and benefits of providing this care (Chase 1980; Houston & Davies 1985; Winkler 1987).

Clutch size is a female trait which males have little possibility of influencing directly. Hence, optimal clutch size will reflect the costs and benefits to females. However, these costs and benefits will depend on the amount of investment males provide and it is therefore important to consider the social context in which clutch size evolves (Svensson & Sheldon 1998). In other words, the optimal clutch size for a female will depend on the expected care of the male (Houston & Davies 1985; Westneat *et al.* 1990; Smith 1995). On the other hand, clutch size strongly affects the male benefit of paternal care and, therefore, male care should depend on the clutch size produced by the female. For example, if a female produces a larger clutch, it may benefit both the male and female to increase their investment (Houston & Davies 1985; Winkler 1987; Beissinger 1990; Wright & Cuthill 1990). Hence, the prevailing mating system may affect the direction of clutch size evolution, but the clutch size may also affect the mating system through its effect on male allocation of investment between parental care

[*]Author for correspondence (henrik.smith@zooekol.lu.se).

2163

and mate attraction. Therefore, there will be joint evolution of clutch size and mating system.

In this paper, we model the joint evolution of parental care and clutch size under sexual conflict. We do this by developing and extending an earlier model of the division of parental care (Houston & Davies 1985). First, we show that, if males have greater opportunities of finding additional mates, males' decision of whether to care for offspring or not should depend on clutch size. Then we show that the female fitness gradient on clutch size (which dictates the future course of clutch size evolution) depends on whether or not males care. The predicted evolutionarily stable clutch size may therefore depend on the initial clutch size. The main results are that the prevailing mating system affects optimal clutch size, that evolution of clutch size will stabilize the mating system and that, under certain circumstances, the resulting combination of mating system and optimal clutch size may be the result of initial conditions.

2. MODELS

(a) *The general model*

The fitness of a reproducing individual is the sum of its returns from the current and all future reproductive events. Assuming that reproduction is costly (Williams 1966; Bell & Koufopanou 1986), optimization of investment in offspring involves trading investment in current reproduction against the cost incurred in the form of lost future opportunities for reproducing. For seasonally reproducing animals, this loss may occur in the same and/or future seasons. A simple fitness function (λ) for describing this is

$$\lambda = nc(x) + p(x, n), \tag{1}$$

where n is the current clutch size, c is juvenile survival and p is the sum of all future reproductive output. Each amount of parental investment (x) received increases the young's survival positively whereas the parent's future fitness prospect decreases with both the size of their investment per young and the size of the current clutch.

In situations where resources for reproduction are limited, the optimum amount of help provided to an offspring will often be related to clutch size (Winkler 1987). Formally, under the assumption that parental care is optimized in ecological (behavioural) time, there is a function $x^*(n)$ that solves $\lambda'(x) = 0$ and $\lambda''(x) < 0$. To begin with, we will consider a mating system where only females care for the young and denote a single female's optimized care as $x_s^*(n)$ (see Appendix A for a derivation). In such a mating system, the optimal clutch size which maximizes lifetime reproductive success (λ) must be calculated as the optimum n (henceforth n_1^*) of

$$\lambda = nc(x_s^*(n)) + p(x_s^*(n), n). \tag{2}$$

In order to be meaningful, this clutch size must not give a negative optimum parental investment, that is $x_s^*(n_1^*)$ must be greater than or equal to zero. This gives the optimum clutch size under the assumption of optimized behaviour.

Because there are two parents, there will be sexual conflict over parental investment that may be resolved by (i) stable biparental care, (ii) female care only, (iii) male care only, or (iv) unstable biparental care where one or the other of the parents may care, the solution being dependent on the initial conditions (Ratnieks 1996). When both parents provide parental care there will be conflict over the amount of investment each sex provides. This is because, if either of the parents decides to increase their investment, the other may decrease its investment and gain higher future fitness (Houston & Davies 1985; Winkler 1987; Wright & Cuthill 1989; Motro 1994; Sozou & Houston 1994). This evolutionary game has traditionally been modelled assuming a single decision rather than using evolutionary stable negotiation rules. It has been shown that evolutionary stable negotiation rules result in parents being less responsive to variation in the effort of the other sex and a lower total level of parental effort (McNamara *et al.* 1999). However, the basic properties of the original model of Houston & Davies (1985) were preserved when remodelling it using stable negotiation rules, namely that parents partially respond to the effort of the other parent and that the outcome is affected by sexual differences in the costs and benefits of providing care (McNamara *et al.* 1999). For mathematical tractability we therefore use the traditional approach of Chase (1980), Houston & Davies (1985), Winkler (1987) and others.

With biparental care, male and female fitnesses can be expressed, respectively, as

$$\lambda_m = nc(x, y) + p(y, n)r, \tag{3}$$

and

$$\lambda_f = nc(x, y) + p(x, n), \tag{4}$$

where y is male investment and r scales alternative male mating opportunities relative to females. These alternative options, besides investing in the current brood, are often different for males and females (Trivers 1972; Emlen & Oring 1977; Arnold & Duvall 1994). The important thing in our model is that r quantifies the sexual difference in the rate of lost fitness through alternative opportunities, capturing the fact that an increase in paternal investment may decrease his future opportunities more than an equivalent increase would decrease those of a female (Queller 1994). For example, males may easily increase their fitness through extra-pair copulations or by attracting additional mates and these opportunities are likely to be lowered with an increased current investment (y). With the formulation used in equations (3) and (4) $r = 1$ means that male and female fitnesses through alternative opportunities are equally affected by providing parental care and $r > 1$ means that males' fitness through alternative opportunities is more sensitive to changes in investment than that of females. In the following we will only analyse situations where $r \geqslant 1$, that is situations with equal or conventional sex roles.

The optimum clutch size (n_2^*) with biparental care maximizes the female fitness equation, i.e.

$$\lambda_f = nc(x^*(n), y^*(n)) + p(x^*(n), n). \tag{5}$$

This optimum n_2^* must of course also allow stable biparental care, that is $x^*(n_2^*)$ and $y^*(n_2^*)$ must both be higher than zero. Otherwise one of the parents will not care for the young and the optimum clutch (n_2^*) calculated from equation (5) can never persist in the population.

Table 1. *Conditions under which different mating systems are stable*

(For brevity, we use the symbol M below instead of the expression $kA + \theta + \ln(\mathcal{J}k/V\theta)$. For explanations of other symbols, see § 2(b).)

| | $r = 1$ | $1 < r$ | |
		$0 < A < M(k + \theta n)$	$0 < M(k + \theta n) < A$
none cares	$\theta(nA - 2) < 2\ln(\mathcal{J}k/V\theta)$	not possible	$2\ln(\mathcal{J}k/V\theta) - n(r) < \theta(nA - 2)$
duck ESS	not possible	$M < (1 + k/n\theta)\ln(r)$	not possible
biparental care	$2\ln(\mathcal{J}k/V\theta) < \theta(nA - 2)$	$(1 + k/n\theta)\ln(r) < M$	$\theta(nA - 2) < 2\ln(\mathcal{J}k/V\theta) - n(r)$

(b) *A specific model*

In order to illustrate how clutch sizes will evolve and converge to the fitness optimum value under the above model, we will use a specific model developed for describing bird provisioning of dependent nestlings (Houston & Davies 1985) because of its mathematical tractability. As above, male investment in an offspring is y and female investment is x. Offspring survival is $c(x, y) = \mathcal{J}(1 - \exp(-k(x + y - A)))$ and adult future opportunities for reproducing are a function of their own investment (i), i.e. $p(i) = V(1 - \exp(-\theta(1 - n)))$, where $\mathcal{J}$ and V are survival constants and θ and k are shape parameters relating survival to parental investment. With these forms the offspring survival probability is zero if total parental investment is below a minimum necessary level (A). Thereafter survival increases with parental investment, but with diminishing returns. The offspring survival function implicitly assumes that there is no interaction between the parents, i.e. that offspring survival is the same irrespective of how a certain amount of investment is partitioned between parents. Parental future reproduction decreases in an accelerating way with parental investment, which in the original model was an effect of decreased survival probability until the following season, but we give p a wider interpretation and include also future reproductive opportunities in the form of other mates the same season. It should be noted that n does not influence future survival if the female provides no parental care (unless $x > 0$). Hence, it is assumed that nestling provisioning and not the production of the clutch constitutes the major reproductive cost. Given that parental investment in young is costly, this simplification does not alter the qualitative predictions, which is why we have kept it in this original form.

3. RESULTS

(a) *Stable mating systems*

Here we explain how the game between parents is solved in behavioural time, thereby resulting in a stable combination of male and female parental investment for a given clutch size. Besides a biparental care evolutionary stable strategy (ESS) we will, with terminology borrowed from Maynard Smith's (1977) classic paper, call a solution where the male leaves the clutch and the female takes care of the young a 'duck' ESS. With $r \geqslant 1$ the specific formulations used here do not allow stability of male-only care or unstable single-parent care (Ratnieks 1996).

First, we consider a case where only females care for the young. We obtain the fitness equation (λ_{fs}) of the female from equation (1) by using the specific forms of

$c(x, 0)$ and $p(x, n)$ in this expression (see Appendix A). The parental investment that maximizes fitness (x_s^*) (see Appendix A) is found where $\lambda'_{\text{fs}}(x) = 0$ and $\lambda''_{\text{fs}}(x) < 0$. The second case is the mating system in equations (3) and (4) which describes biparental care and is in principle a game between parents played on a behavioural time-scale. The game was originally analysed by Houston & Davies (1985) and we briefly review the solution here. Formally, the model is a two-player, asymmetrical game where the continuous strategy sets are $y \geqslant 0$ and $x \geqslant 0$ for the male and female, respectively. Each parent will adjust its provisioning in relation to the contribution of their partner and the male has a y strategy that maximizes his fitness for a given x strategy of the female and vice versa for the female. These are therefore called 'best reply' strategies in order to capture the fact that they are the best replies to a given action of the 'opponent'. The solution to the game is a combination (y^*, x^*) of male and female investment that is evolutionarily stable in the sense that y^* is a best reply to x^* and x^* is a best reply to y^* (Maynard Smith 1982; Motro 1994). The analysis of the game and the simultaneous solutions of optimum male and female care are given in Appendix A. The necessary conditions for all mating systems considered are listed in table 1. If $r = 1$, males and females have equal alternative opportunities besides investing in the current brood and the only possible solutions to the parental game are that both parents should provide care or that neither of them should (table 1). If $r > 1$ there are stable solutions where neither of the parents should provide care to offspring, where only the female should provide care and where both parents should provide care. Which case applies depends on the level of A, the minimum necessary amount of care and also on clutch size as this influences the optimum investment of males. Male optimum investment, i.e. $y^*(n)$, is zero for low clutch sizes (n), but with a larger clutch $y^*(n)$ increases above zero so that males should care only if n is higher than a certain value, β (see Appendix A). If the clutch size is below this value, the optimum female care is given by x_s^*. If $r > 1$, there is no solution where only males care—if males care so do females. For very large clutch sizes, there may be a solution whereby neither of the parents care for their young (see Appendix A).

(b) *Dependency on clutch sizes*

The conditions for the different mating systems in table 1 contain clutch size as a parameter, that is, with a certain clutch size and a set of values for the other parameters, only one mating system is stable. However, in any given mating system clutch size is expected to evolve, which may have consequences for the mating system as
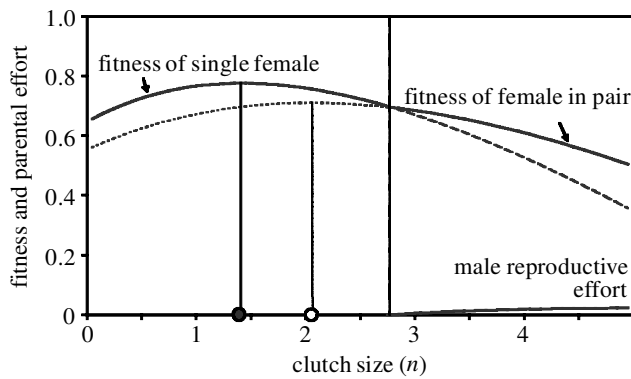
Figure 1. Optimum clutch sizes for single females and paired females when only a single female optimum is possible. The upper curved lines show the realized female fitness. Male care is only positive for high clutch sizes. Females always care in this case. From an initial condition with biparental care and a large clutch, smaller clutches will invade the population. Eventually males will be better off if not caring for young and then the clutch size evolves to the optimum for single females. The hatched line shows the fitness of the female if the male behaves suboptimally and does not care for the young. The dotted curved line is a solution that involves negative male care and is therefore of no biological importance. $A = 0.15$, $k = 4.2$, $\theta = 2.4$, $\mathcal{J} = 0.35$, $V = 0.7$ and $r = 6$.
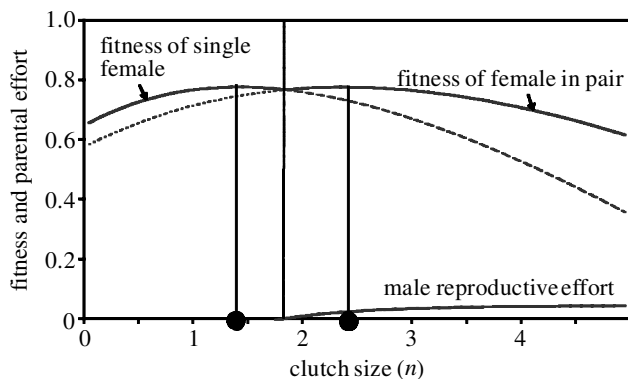

Figure 2. Two solutions are simultaneously stable, i.e. duck and biparental care ESSs. The position of the threshold β is shown by the vertical dotted line. If the clutch size is initially above this value, a biparental care mating system will evolve (right-hand closed circle), whereas if the clutch size is initially below this value, a duck mating system with a lower clutch size will evolve. $A = 0.15$, $k = 4.2$, $\theta = 2.4$, $\mathcal{J} = 0.35$, $V = 0.7$ and $r = 4.5$.

the male and female optimum parental investments (y^* and x^*) are both functions of clutch size. For example, all else being equal, an increase in clutch size may change the stable mating system from a 'duck' ESS to biparental care (table 1) (if $r > 1$ and $0 < A < M(k + \theta n)$). Thus, in order to deduce the stable parental investment pattern, clutch size evolution must be taken into account, which brings us to the main object of our analysis.

In order to illustrate the different possible simultaneous solutions of stable clutch size and parental care, we have chosen to plot fitness equations (2) and (5) simultaneously with our specific forms of (c) and (p) and the stable levels of male help as functions of clutch size (figures 1–3). We focus on the case with higher male than female alternative mating opportunities ($1 < r$) and with A low enough that a
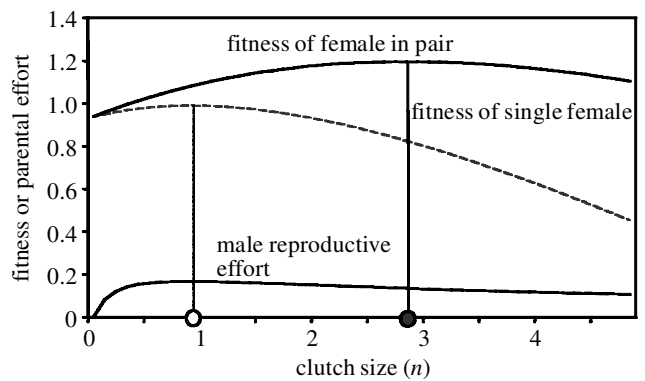

Figure 3. As figure 2, but with a lower r. Note that the threshold value for male help (β) (vertical dotted line) is lower than the optimum clutch size of a single female (open circle). Only the higher optimum with biparental care is possible in this case. $A = 0.15$, $k = 4.2$, $\theta = 2.4$, $\mathcal{J} = 0.35$, $V = 0.7$ and $r = 3$.

single female could successfully rear at least one offspring without male help. There are then three possible solutions (see Appendix A): (i) only single female care and a small clutch size can be stable (figure 1), (ii) only biparental care with a large clutch size can be stable (figure 3), or (iii) both solutions may be stable simultaneously (figure 2). The stability of the equilibria is determined by the value of the break-point clutch size (β), below which male optimum care is zero. Above this value males should provide at least some care for the young. At β, females in pairs and single females have equal fitnesses (because males do not provide paternal care in either situation). With all higher clutch sizes, paired females will have higher fitness than if males abandon the clutch (although this behaviour of the male would be contrary to our assumption of optimized behaviour) because the males will provide care.

We show in Appendix A that, if β does not exist, males will never care and the only possible optimum in this case is a duck ESS. One important reason why β might not exist is that r is high, which may occur when males lose alternative mating opportunities much faster than females with increasing investment in their current brood than females. A duck ESS is also the only solution if r is smaller, so that β does exist but is so high that it is above the biparental care ESS optimum clutch size (figure 1). With still lower r, β is in-between the optimum clutch size for duck and biparental care ESSs (figure 2). In this case both duck and biparental care ESSs are possible solutions. The one which actually evolves is determined by the initial conditions. If the clutch size is initially above β, biparental care will evolve, whereas if it is initially below β, a duck ESS evolves. Further decreasing r brings β below the duck optimum clutch size (figure 3) and then only biparental care can be stable.

4. DISCUSSION

Our model demonstrates that the conflict between males and females over the division of parental care will have a major influence on the evolution of clutch size. The effect of parent–offspring conflict on the evolution of clutch size was investigated by Godfray & Parker (1991) in an earlier study. In this paper, we demonstrate how the
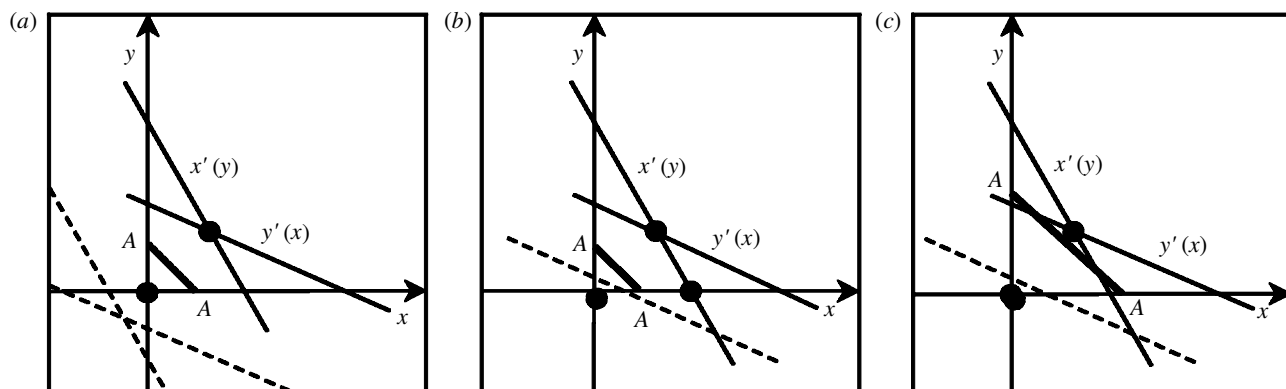
Figure 4. Graphs showing the intersections between the best reply curves $y'(x)$ and $x'(y)$. The stable solutions to the parental investment game are shown with closed circles. The thick A line shows the minimum summed male and female investment for offspring survival. (a) $r = 1$. If the best reply curves intersect below the A line the solution is $(0, 0)$ (hatched lines). If the sum of male and female care at the intersection is higher than A the solution is biparental care. (b) $r > 1$ and A is low. If the reply curves intersect in the third quadrant the solution is a duck ESS. If the best reply curves intersect in the first quadrant the solution is (x^*, y^*) (biparental care). (c) $r > 1$ and A is high. If the sum of male and female care at the intersection is higher than A, the solution is biparental care. If the best reply curves intersect at a point where $x^* + y^* < A$ the solution is no care. The mathematical conditions for the different solutions are given in table 1.

sexual conflict over clutch size is resolved and that the resulting clutch size may be different than when assuming no conflict. Thus, our model extends the results of Houston & Davies (1985).

The important assumptions of our model are that male care becomes more valuable as clutch size increases and that males, at least in evolutionary time, adjust how much paternal care they provide to the opportunity costs paid. In a non-manipulative study of the dunnock (*Prunella modularis*), male help became increasingly important for reproductive success as the number of hatchlings increased (Davies & Hatchwell 1992). Although we are not aware of any study where brood size manipulations and male removals have been performed simultaneously, numerous studies have shown that males do respond to increased brood size with increased parental effort (Clutton-Brock 1991). Furthermore, Wright & Cuthill (1990) demonstrated that experimentally altered male care in European starlings (*Sturnus vulgaris*) had a larger effect on the female workload when brood size was larger. Several studies have directly demonstrated that males do adjust their investment in current offspring in relation to the availability of mates (Keenleyside 1983; Clutton-Brock 1991; Smith 1995) or extra-pair partners (Magrath & Elgar 1997) and such differences also exist between species (Wittenberger 1981). Hence, the basic requirements for the model seem to be fulfilled.

Because female genes determine clutch size and males have little opportunity of influencing clutch size directly, this trait will evolve to the optimum value of females. However, the optimal clutch size from a female's perspective will depend on the amount of paternal care her mate is expected to provide. This is because, if a male cares, it enables females to lower their investment in each young, thereby changing the female fitness gradient on clutch size. The sexual conflict over parental care will in turn be affected by clutch size since a larger clutch makes male care more valuable. Therefore, there will be joint evolution of mating system and clutch size.

Searcy & Yasukawa (1995) proposed that a mating system and the need for male parental care should coevolve, but excluded clutch size from consideration since it was unclear which sex ought to win the conflict over clutch size. However, when male and female optimum parental investment is calculated by assuming a sexual game where each parent provides care in proportion to the contribution of the partner, males should provide care if the clutch size is higher than a certain value, i.e. β. This threshold value is a function of two factors: (i) the value of paternal care to the survival of offspring, and (ii) the extent to which parental care affects the opportunity of achieving additional matings (Westneat *et al.* 1990; Webster 1991). At the same time, the evolutionary stable clutch size will depend on the amount of parental care males provide. Thus, the outcome of sexual conflict depends on the sexual difference in the costs and benefits of raising young.

A different way of expressing the result is that clutch size evolution will tend to stabilize mating systems. When β is lower than the optimum clutch for a duck mating system (figure 3), then all initial clutch sizes eventually evolve into the one with biparental care. On the other hand, only a duck ESS is possible when $r > 1$ and the break-point value β is above the optimum clutch for biparental care (figure 1). Then all initial clutch sizes will end with single female investment in the young and relatively small clutch sizes. As an outcome of this coevolution, we would expect an association between clutch size, paternal care and mating system (Silver *et al.* 1985).

Clutch size and the extent to which males provide care will thus coevolve over evolutionary time such that male help will be of value to the female in circumstances when it is provided. Hence, male removal experiments (Wolf *et al.* 1988; Bart & Tornes 1989) will tell us little about why male parental care originally evolved (cf. Westneat *et al.* 1990). The effect of paternal care on alternative mating opportunities may differ if these opportunities are extra-pair copulations or additional mates (Westneat *et al.* 1990). Factors such as female dispersion, breeding

synchrony and the predation rate will affect the operational sex ratio and, therefore, have a major influence on the availability of mates (Trivers 1972; Emlen & Oring 1977; Wittenberger 1981). Male decisions may also feed back on r, the sensitivity of opportunity costs to male help, for example, because different mating systems create different opportunities for finding alternative mates.

Under certain circumstances (figure 2) the expected clutch size and mating system will depend on the initial conditions, that is what clutch size prevailed in the population to start with. According to the model, an initial state where males provide some care for the young may select in favour of females increasing their clutch size. With higher clutch size males should increase their investment in young so that females will evolve still higher clutch sizes and so on until a stable state is reached where males give rather a lot of help and clutch sizes are relatively high. On the other hand, if clutch sizes are smaller to begin with (below β) (figure 2) males should not help at all. Females would then be selected in favour of decreasing their clutch size so that there would be even less benefit for males in helping and the end-point would be a small clutch with only females caring for the young. Here the break-point (β) separates mating systems into either duck or biparental help ESSs.

This scenario could tentatively result in major differences in clutch size and mating system between populations because of slightly different initial conditions. However, it may be difficult to infer such historic events given the fact that clutch size (or other factors governing the need for parental care) (cf. Searcy & Yasukawa 1995) will coevolve and stabilize the mating system. Thus, two populations that have evolved to different mating systems because of historical reasons only will nevertheless demonstrate differences in the value of male parental care to female fitness.

The results in this paper stress the importance of taking sexual conflict into consideration when modelling the evolution of clutch size. However, the evolution of other life-history variables may also be affected by sexual conflict. For example, by choosing which time of the season to produce a clutch, females may adjust the peak demand of nestlings to the seasonal availability of food, but at the same time this decision affects how polygynous males allocate investment between different broods (Slagsvold & Lifjeld 1994; Smith & Sandell 1998) or males' opportunities for searching for additional mates (cf. Slagsvold & Lifjeld 1989). Furthermore, the asynchrony of hatching dates within a clutch may be an important fitness-determining factor in cases where it has an effect on male provisioning. In some cases males may provide more care to asynchronous broods (Slagsvold & Lifjeld 1989) and, in these cases, hatching asynchrony has been put forward as a female trait for taking advantage of males which males will have little power of influencing. However, other experiments have shown that males increase their investment in synchronous broods (Slagsvold *et al.* 1994; Slagsvold 1997). This suggests that male care and hatching asynchrony will coevolve in much the same way as in the case of the clutch size presented above, but that coevolution may take place in many different ways. Thus, the interaction between life-history traits and the sexual conflicts associated with the social context may be complex and take different forms in different cases.

APPENDIX A

(a) *Mating systems and optimum parental care*

Assume that the female takes care of the offspring alone. Then the fitness equation of the female from equation (1) with our specific forms of $c(x)$ and $p(x, n)$ takes the form

$$\lambda_{fs} = n\mathcal{J}(1 - e^{-k(x-A)}) + V(1 - e^{-\theta(1-nx)}). \tag{A1}$$

The optimum care (x_s^*) of females solves $\lambda_{fs}'(x) = 0$ (condition for singular point) and $\lambda_{fs}''(x) < 0$ (for maximum) and is

$$x_s^*(n) = \frac{kA + \theta + \ln\left(\dfrac{\mathcal{J}k}{V\theta}\right)}{k + \theta n}. \tag{A2}$$

If both parents provide care to the young, each one should provide in relation to how much the other parent is investing. The investment $y'(x)$, which maximizes male fitness for a given investment by the female, is called his best reply (Motro 1994) This function is obtained from equation (3) by solving $\lambda_m'(y) = 0$ for y and checking that $\lambda_m''(y) < 0$ is true for the solution. The female's best reply can be obtained from equation (4) in an equivalent way by differentiating with respect to x. The male and female best replies are, respectively,

$$y'(x) = \frac{kA + \theta + \ln\left(\dfrac{\mathcal{J}k}{V\theta}\right) - \ln(r) - kx}{k + \theta n}, \tag{A3}$$

and

$$x'(y) = \frac{kA + \theta + \ln\left(\dfrac{\mathcal{J}k}{V\theta}\right) - ky}{k + \theta n}. \tag{A4}$$

Both of these equations are decreasing linear functions and it is therefore easy to find the solution (x^*, y^*) to the game from the intersection of the best reply curves (figure 4). The mathematical expressions of optimum male (y^*) and female care (x^*) at this stable equilibrium are solved from the following simultaneous equations which are the derivatives of equations (3) and (4). In order to ensure that the solution defines a fitness maximum, the second derivatives of equations (3) and (4) must be negative.

$$\begin{cases} n\dfrac{\partial c}{\partial y}(x^*, y^*) + r\dfrac{\partial p}{\partial y}(y^*, n) = 0 \\[2mm] n\dfrac{\partial c}{\partial x}(x^*, y^*) + \dfrac{\partial p}{\partial x}(x^*, n) = 0 \end{cases}. \tag{A5}$$

The solutions turn out to be the following functions of clutch size:

$$y^*(n) = \frac{kA + \theta + \ln\left(\dfrac{\mathcal{J}k}{V\theta r}\right) - \dfrac{k}{\theta n}\ln(r)}{2k + \theta n}, \qquad (A6)$$

and

$$x^*(n) = \frac{kA + \theta + \ln\left(\dfrac{\mathcal{J}k}{V\theta}\right) + \dfrac{k}{\theta n}\ln(r)}{2k + \theta n}. \qquad (A7)$$

Let $M = kA + \theta + \ln(\mathcal{J}k/V\theta)$. If $M < 0$ neither of the best replies is positive and the only solution is $(x^*, y^*) = (0, 0)$. With positive M, the solutions depend on the level of A, the minimum requirement of investment for positive offspring survival. If $x^* + y^* < A$ the offspring survival probability is zero so that parents are predicted not to care for their offspring and the solution is again $(0, 0)$. From this condition it can be shown that, if $0 < M$ and $r = 1$, the solution is biparental care (figure 4a) if $2\ln(\mathcal{J}k/V\theta) < \theta(nA - 2)$. The reverse is the condition for no care. If $r > 1$ and A is low so that $0 < A < M/(k + \theta n)$, the intersection of the best reply curves is in the fourth quadrant if $M < (1 + k/\theta n)\ln(r)$ (figure 4b). The solution in this case is a duck ESS and the alternative if $(1 + k/\theta n)\ln(r) < M$ is biparental care. If $r > 1$ and A is high so that $0 < M/(k + \theta n) < A$ (figure 4c), $A < x^* + y^*$ for only some of the intersections in the first quadrant (above the thick 'A' line in figure 4c). As we assume that $x^* + y^* < A$ means zero offspring survival and no parental care, we obtain the condition for biparental care, i.e. $\theta(nA - 2) < 2\ln(\mathcal{J}k/V\theta) - \ln(r)$. The reverse is the condition for no care.

We now take a closer look at the case $r > 1$ and $0 < A < M/(k + \theta n)$ where we had the alternative solutions, i.e. a duck ESS or biparental care. If the male alternative mating opportunities are higher than those of the female, the optimum care for the male is positive (i.e. $y^*(n) > 0$) provided that the clutch size is larger than a certain β-value which is given by

$$\beta = \frac{k\ln(r)}{\theta(kA + \theta + \ln(\mathcal{J}k/V\theta) - \ln(r))}. \qquad (A8)$$

The total amount of care an offspring then receives is the sum of male and female care which is

$$y^*(n) + x^*(n) = \frac{2kA + 2\theta + 2\ln\left(\dfrac{\mathcal{J}k}{V\theta}\right) - \ln(r)}{2k + \theta n}. \qquad (A9)$$

This summed parental care is higher than that which a single female provides (equation (A2)) if the clutch size is higher than β, i.e. always with positive male care. In addition, a female in a pair situation provides less care than a single female (equation (A7) < equation (A2)) if the clutch size is higher than β, again always with male care. From this it follows that, with a clutch size higher than β, females in pairs always have higher fitness than single females. With lower clutch sizes, male help is not stable. In summary, there are three possible situations with respect to the position of β relative to the humps of the fitness curves of single and paired females and these are shown in figures 1–3. Either β is high so that the only stable point is single female care (figure 1) or, if β is

somewhat lower, it may be in-between the optimum clutch sizes of single and paired females (figure 2) which are both stable. With still lower β only biparental care can be stable (figure 3).

(b) *Finding the optimum clutch size*

First, consider the case when only females care for the young. Equation (2) is the fitness equation of the female. The clutch size (n_1^*) that maximizes fitness is then found by differentiating equation (2) with respect to n, setting the result equal to zero and solving for clutch size.

$$\frac{d\lambda_{\mathrm{fs}}}{dn} = c(x_s^*(n)) + n\frac{\partial c}{\partial x_s^*}\frac{\partial x_s^*}{\partial n} + \frac{\partial p}{\partial x_s^*}\frac{\partial x_s^*}{\partial n} + \frac{\partial p}{\partial n} = 0. \qquad (A10)$$

In order to ensure that n_1^* is a maximum point, the second derivative of equation (2) must be negative. We were not able to solve this explicitly, but chose a graphical solution instead. In the same way, in a mating system where both parents care for young, the fitness equation for maximizing is equation (5).

$$\frac{d\lambda_{\mathrm{f}}}{dn} = c(x^*(n), y^*(n)) + n\left[\frac{\partial c}{\partial x^*}\frac{\partial x^*}{\partial n} + \frac{\partial c}{\partial y^*}\frac{\partial y^*}{\partial n}\right] + \frac{\partial p}{\partial x^*}\frac{\partial x^*}{\partial n} + \frac{\partial p}{\partial n} = 0. \qquad (A11)$$

Again, the value n_2^*, which solves equation (A11), is a maximum given that the second derivative is negative.

REFERENCES

Arnold, S. J. & Duvall, D. 1994 Animal mating systems: a synthesis based on selection theory. *Am. Nat.* **143**, 317–348.

Bart, J. & Tornes, A. 1989 Importance of monogamous male birds in determining reproductive success. Evidence for house wrens and a review of male-removal studies. *Behav. Ecol. Sociobiol.* **24**, 109–116.

Beissinger, S. R. 1990 Experimental brood manipulations and the monoparental threshold in snail kites. *Am. Nat.* **136**, 20–38.

Bell, G. & Koufopanou, V. 1986 The cost of reproduction. In *Oxford surveys of evolutionary biology* (ed. R. Dawkins & M. Ridley), pp. 83–131. New York: Oxford University Press.

Chase, I. D. 1980 Cooperative and noncooperative behavior in animals. *Am. Nat.* **115**, 827–857.

Clutton-Brock, T. H. 1991 *The evolution of parental care.* Princeton University Press.

Cucco, M. & Malacarne, G. 1997 The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros. Ardea* **85**, 211–221.

Davies, N. B. & Hatchwell, B. J. 1992 The value of male parental care and its influence on reproductive allocation by male and female dunnocks *Prunella modularis. J. Anim. Ecol.* **61**, 259–272.

Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

Godfray, H. C. J. & Parker, G. A. 1991 Clutch size, fecundity and parent–offspring conflict. *Phil. Trans. R. Soc. Lond.* B **332**, 67–79.

Hasselquist, D. & Bensch, S. 1991 Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. *Behav. Ecol. Sociobiol.* **28**, 187–193.

Houston, A. I. & Davies, N. B. 1985 The evolution of cooperation and life history in the dunnock, *Prunella modularis.* In *Behavioural ecology: ecological consequences of adaptive behaviour* (ed. R. Sibly & R. Smith), pp. 471–487. Oxford, UK: Blackwell Scientific Publications.

Keenleyside, M. H. A. 1983 Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* **31**, 683–688.

Lack, D. 1947 The significance of clutch size. *Ibis* **89**, 302–352.

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999 Incorporating rules for responding into evolutionary games. *Nature* **401**, 368–371.

Magrath, M. J. L. & Elgar, M. A. 1997 Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc. R. Soc. Lond.* B **264**, 1731–1736.

Maynard Smith, J. 1977 Parental investment: a prospective analysis. *Anim. Behav.* **25**, 1–9.

Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.

Motro, U. 1994 Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. *Am. Nat.* **144**, 229–241.

Queller, D. C. 1994 Male–female conflict and parent–offspring conflict. *Am. Nat.* **144**, 84–99.

Ratnieks, F. L. W. 1996 Evolution of unstable and stable biparental care. *Behav. Ecol.* **7**, 490–493.

Roff, D. A. 1992 *The evolution of life-histories: theory and analysis*. New York: Chapman & Hall.

Searcy, W. A. & Yasukawa, K. 1995 *Polygyny and sexual selection in red-winged blackbirds*. Princeton University Press.

Silver, R., Andrews, H. & Ball, G. F. 1985 Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am. Zool.* **25**, 823–840.

Slagsvold, T. 1997 Is there a sexual conflict over hatching asynchrony in American robins? *Auk* **114**, 593–600.

Slagsvold, T. & Lifjeld, J. T. 1989 Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. *Am. Nat.* **134**, 239–253.

Slagsvold, T. & Lifjeld, J. T. 1994 Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* **143**, 59–94.

Slagsvold, T., Amundsen, T. & Dale, S. 1994 Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature* **370**, 136–138.

Smith, H. G. 1995 Experimental demonstration of a trade-off between mate attraction and paternal care. *Proc. R. Soc. Lond.* B **260**, 45–51.

Smith, H. G. & Sandell, M. I. 1998 Intersexual competition in a polygynous mating system. *Oikos* **83**, 484–495.

Sozou, P. D. & Houston, A. I. 1994 Paternal effort in a mating system involving two males and two females. *J. Theor. Biol.* **171**, 251–266.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Svensson, E. & Sheldon, B. C. 1998 The social context of life history evolution. *Oikos* **83**, 466–477.

Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man* (ed. B. Campbell), pp. 52–97. Chicago, IL: Aldine Publishing Co.

Webster, M. S. 1991 Male parental care and polygyny in birds. *Am. Nat.* **137**, 274–280.

Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990 The ecology and evolution of extra-pair copulations in birds. In *Current ornithology*, vol. 7 (ed. D. M. Power), pp. 331–369. New York: Plenum Press.

Whittingham, L. A. 1993 Effects of nestling provisioning on the time-activity budgets of male red-winged blackbirds. *Condor* **95**, 730–734.

Whittingham, L. A. 1994 Additional mating opportunities and male parental care in red-winged blackbirds. *Anim. Behav.* **48**, 875–883.

Williams, G. C. 1966 Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690.

Winkler, D. W. 1987 A general model for parental care. *Am. Nat.* **130**, 526–543.

Wittenberger, J. F. 1981 *Animal social behavior*. Boston, MA: Duxbury Press.

Wolf, L., Ketterson, E. D. & Nolan, V. J. 1988 Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Anim. Behav.* **36**, 1601–1618.

Wright, J. & Cuthill, I. 1989 Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* **25**, 171–181.

Wright, J. & Cuthill, I. 1990 Manipulation of sex differences in parental care: the effect of brood size. *Anim. Behav.* **40**, 462–471.