Mate availability influences filial cannibalism in fish with paternal care

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In fish with paternal care, males often eat their offspring (i.e. filial cannibalism). This is regarded as a male's adaptive strategy to maximize lifetime reproductive success by enhancing his own survivorship or the survivorship of the remaining offspring at the cost of current reproductive success. Although the parental energy reserve has been considered a primary factor influencing filial cannibalism, the possibility that mate availability may also be an important factor has been overlooked. When many mates are available, males may receive a surplus of eggs, which can be treated as an energy reserve and reallocated to future breeding attempts. We present a game theoretical model for the evolution of filial cannibalism, incorporating intrinsic parental condition and extrinsic breeding system components which determine mate availability. The model predicts that filial cannibalism is favoured under the following conditions: (1) the male's energy reserve is low; (2) mate search efficiency is high; (3) the population density is high; (4) the sex ratio is female biased; (5) the male care period is long; and (6) the female's refractory period is short. Conditions 2–6 facilitate filial cannibalism through an increase in mate availability.

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Filial cannibalism is especially widespread in fish (Hausfater & Hrdy 1984; Elgar & Crespi 1992). Early ethologists regarded it as a social pathology because it was often found in unusually artificial conditions and because it seems to counter the traditional 'Darwinian view' that parents should endeavour to increase offspring survival. However, as a number of studies have documented filial cannibalism in nature, it is now considered adaptive (Dominey & Blumer 1984; FitzGerald 1992; FitzGerald & Whoriskey 1992).

Rohwer (1978) was first to propose an adaptive explanation of filial cannibalism in species with paternal care. Parental males, which are often food limited, should parasitize female gametic investment as an alternative energy source, thereby enhancing their own survivorship, or the survivorship of the remaining offspring in cases in which their clutches are partially consumed. Filial cannibalism could therefore evolve when such future benefits from offspring consumption outweigh the loss of present reproduction. Rohwer's (1978) hypothesis leads to a prediction that filial cannibalism should increase as parental

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energy reserves decrease (Sargent 1992; Sargent et al. 1995), as supported by empirical studies (DeMartini 1987; Belles-Isles & FitzGerald 1991; Marconato et al. 1993; Okuda & Yanagisawa 1996a; Lindström 1998).

Mate availability may be another important factor influencing filial cannibalism by males (Okuda & Yanagisawa 1996b; Okuda 1999, 2000). When mate availability is high, males can easily obtain eggs from additional females. In this situation, eggs lost to filial cannibalism can be replaced in additional matings, or the energy provided by a surplus of eggs can be reallocated to future reproduction through improved parental survival. Therefore, filial cannibalism should become more frequent with increasing mate availability. Following this argument, it might be expected that filial cannibalism can be influenced not only by paternal condition but also by breeding system components such as sex ratio, number of mates in a breeding cycle and parental expenditure by both sexes. This is because these factors are major determinants of the operational sex ratio, and thus have a large effect on mate availability (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Parker & Simmons 1996; Reynolds 1996; Székely et al. 2000).

Some theoretical studies have attempted to examine conditions favouring filial cannibalism (Sargent 1992; Sargent et al. 1995; Lindström 2000). They showed that

parental status plays an important role in determining filial cannibalism. However, there are some unanswered questions. First, some previous models either assume that mates are constantly available to males (Sargent 1992; Sargent et al. 1995) or overlook the relationship between mate availability and breeding system components (Lindström 2000). Such models cannot reveal how the breeding system components influence filial cannibalism. To examine this problem, the effects of breeding system components on mate availability should be incorporated in a model.

Furthermore, it remains unclear how the behaviour of other members in the population influences the adaptive behaviour of the focal individual through changes in mate availability (Sargent 1992; Sargent et al. 1995). Once filial cannibalism is adopted by the majority of males in a population, it could decrease mate availability for males because cannibalistic males remain sexually receptive but exploited females enter the refractory phase to replenish their eggs (Smith & Wootton 1995; but see Kvarnemo 1998). In such cases, the decrease in mate availability caused by increasing filial cannibalism may inhibit further evolution of filial cannibalism. To reveal the outcome of this interaction between filial cannibalism and mate availability, the game-theoretical situation (Yamamura & Tsuji 1993; Székely et al. 1996, 2000; Balshine-Earn & Earn 1997; Alonzo & Warner 1999, 2000; Kondoh 2001) should be taken into account.

Here we present a game-theoretical model for the evolution of filial cannibalism in paternal care species, which integrates parental status (intrinsic factor) with the effects of breeding system components (extrinsic factor) within a single model (Kondoh 2001). With this model we show how intrinsic and extrinsic factors simultaneously determine filial cannibalism. As possible determinants of filial cannibalism, we deal with the following factors: parental energy reserve; the efficiency of mate search; population density; sex ratio; parental time expenditure by both sexes; and the number of mates in a breeding cycle.

THE MODEL

Consider (kD) males and $\{(1 - k)D\}$ females breeding continuously in a given population, where D is the population density and k ($0 \leq k \leq 1$) is the proportion of males. Sexually receptive males and females search for mates at an efficiency, a, taking a period of s_m and s_f to get a mate, respectively. When individuals of the opposite sex encounter each other, a female gives her entire clutch to a male and then abandons him. After the mating, the female becomes unreceptive for a time R_f during which she replenishes her eggs (i.e. refractory period), while the male continues to advertise to other mates until he receives n clutches. Thereafter, the male enters a sexually inactive phase (i.e. care period) to provide care for a constant number (C) of clutches and cannibalize the remaining (p) clutches ($p = n - C$). The male spends the time R_m on parental care until the last offspring is independent. Males and females become receptive again after the completion of parental care and egg replenishment, respectively, and start the next breeding cycle. The

time required for males to complete a breeding cycle is the sum of time spent on mate search ($n s_m$) and parental care (R_m), that is, $\{(C + p) s_m + R_m\}$.

We assume that male energy reserve (i.e. parental condition), E, increases as the number of clutches cannibalized, p, increases (Lindström & Sargent 1997; Lindström 1998). It can be expressed as $E(p) = E_0 + ep$, where E_0 is the initial energy reserves without cannibalism and e is the energy conversion efficiency. Further assume that the male reproductive gain, $Cw(E)$, increases with his energy reserve, E, where $w(E)$ is a smooth and monotonous increasing function of E with a convex curve from 0 to 1 (i.e. $w(0) = 0$, $w'(E) > 0$, $w''(E) < 0$, $\lim_{E \to \infty} w(E) = 1$). Under these assumptions, we examine the evolutionarily stable number of clutches cannibalized, p^{cs}.

Reproductive Dynamics

First, we determine the male's average search time $s_m^\star$ when most males cannibalize $p^\star$ clutches in a breeding cycle. The value of $s_m^\star$ can be used as an indicator of the availability of females: a small $s_m^\star$ reflects a high mate availability. It is inversely proportional to the mate search efficiency a and the number of receptive females F_s (i.e. $s_m^\star = 1/(a F_s^\star)$). At equilibrium, since all sexually active males mate with females at the same encounter rate (Kondoh 2001), the number of males searching for the i'th female ($m_s^\star(i)$) should be equal for all i ($1 \leq i \leq n$). Thus the total number of receptive males ($M_s^\star$) is the sum of males searching for the i'th female for $i = (1, 2, \ldots, n)$, that is,

$$M_s^\star = (C + p^\star) m_s^\star. \tag{1}$$

At equilibrium, the number of males that enter the receptive phase, $(kD - M_s^\star)/R_m$, should be balanced with the number of males that enter the unreceptive phase, $a m_s^\star F_s^\star$. Hence, it follows that:

$$a m_s^\star F_s^\star = (kD - M_s^\star)/R_m, \tag{2}$$

where the left-hand side of the equation is the number of males that have become unreceptive after acquiring the nth mating per unit time, and the right hand side is the number of males that have finished paternal care per unit time. Similarly, the number of females that become unreceptive after giving their clutch to a male should be balanced with the number of females that become receptive per unit time, that is,

$$a M_s^\star F_s^\star = \{(1 - k)D - F_s^\star\}/R_f. \tag{3}$$

Equations (1), (2) and (3) taken together make

$$(1 - k)D - F_s^\star = \frac{a R_f kD F_s^\star}{1 + \{a R_m F_s^\star/(C + p^\star)\}}. \tag{4}$$

Equation (4) gives $F_s^\star$ as its unique solution at equilibrium (Appendix 1). Subsequently, the average search time for males, $s_m^\star$, is obtained as $s_m^\star = 1/(a F_s^\star)$.

Evolutionary Dynamics

To determine the evolutionarily stable number of clutches cannibalized, p^{cs}, we assume that the time scale of reproductive dynamics is much shorter than that of evolutionary dynamics. Under such an assumption, we can evaluate the dynamics of p^* at the stationary value of s_m^* where equation (4) holds.

When most males cannibalize p^* clutches in a breeding cycle, the fitness of a mutant male with a slightly different strategy p can be given as

$$W_m(p^*, p) = \frac{Cw(E)}{(C+p)s_m^* + R_m},\qquad (5)$$

where $W_m(p^*, p)$ is the reproductive rate of the mutant male, that is, the reproductive gain $Cw(E)$ per one reproductive event that takes $\{(C+p) s_m^* + R_m\}$. This equation implies that, with increasing p, the mutant male increases his reproductive gain $Cw(E)$, but his breeding cycle is prolonged. When the mutant's fitness, $W_m(p^*, p)$, is larger than that of wild-type males, $W_m(p^*, p^*)$, the mutant invades the population and consequently the average number of clutches cannibalized, p^*, shifts towards p. The evolutionary dynamics of p^* is given by examining the gradient of W_m at the stationary value of s_m^*, namely,

$$\frac{dp^*}{dt} = g\left(\frac{\partial \ln[W_m]_{S_m = s_m^{*2}(p^*)}}{\partial p}\bigg|_{p = p^*} \right)\qquad (6)$$

where g represents the intensity of selection (Iwasa et al. 1991; Abrams et al. 1993). We treat the number of clutches cannibalized, p, as a continuous trait in this analysis, although it is discrete in reality. Numerical calculations for a discrete model reveal that this approximation does not make qualitative changes in the results.

RESULTS

The dynamical system governed by equation (6) converges to a unique evolutionary equilibrium $p^{cs} (\geq 0)$. It is obtained by setting the right-hand side of this equation to zero ($dp^*/dt = 0$). This simplifies to the following equation (Appendix 2):

$$Q = (C+p^*) + (R_m/S_m) - (w/w') = 0.\qquad (7)$$

The function Q is a useful indicator to determine whether p^* increases or decreases under a given condition. More frequent cannibalism is favoured (i.e. p^* increases) if Q is positive, while cannibalism becomes less frequent (p^* decreases) if Q is negative (Appendix 2). The Q is a decreasing function of p^* (i.e. $\partial Q/\partial p^* = -(R_m/s_m^{*2})$ $(\partial s_m^*/\partial p^*) + (w\, w''/w'^2) < 0$), and it holds that $\lim_{p^* \to \infty} Q < 0$, implying that there exists a unique solution of p^{cs} if, and only if, it is true that $Q\,|_{p^*=0} > 0$. If not, the equilibrium is that $p^{cs} = 0$.

Equation (7) makes $\partial p^*/\partial E_0 = -(\partial Q/\partial E_0)/(\partial Q/\partial p^*)$. Noting that Q decreases with increasing initial energy reserves, E_0 (i.e. $\partial Q/\partial E_0 = -\partial(w/w')/\partial E_0 < 0$) and that Q decreases with increasing p^* ($\partial Q/\partial p^* < 0$), it follows that the equilibrium number, p^{cs}, of clutches cannibalized decreases with increasing E_0 ($\partial p^*/\partial E_0 < 0$; Fig. 1a).

Equation (7) also makes $\partial p^*/\partial X = -(\partial Q/\partial X)/(\partial Q/\partial p^*) = -\{(\partial Q/\partial s_m^*)\ (\partial s_m^*/\partial X)\}/(\partial Q/\partial p^*)$, where $X = a, D, k, R_m$, or R_f. Noting that Q decreases with increasing mate search time s_m^* ($\partial Q/\partial s_m^* < 0$) and that Q decreases with increasing p^* ($\partial Q/\partial p^* < 0$), it follows that the equilibrium number, p^{cs}, of clutches cannibalized increases with increasing X ($\partial p^*/\partial X > 0$) if the s_m^* decreases with increasing X ($\partial s_m^*/\partial X < 0$), while it decreases ($\partial p^*/\partial X < 0$) if the s_m^* increases with increasing X ($\partial s_m^*/\partial X > 0$). As derived from equation (4) (Appendix 1), the search time, s_m^*, decreases as (1) the efficiency of mate search, a, increases, (2) the population density, D, increases, (3) the sex ratio becomes biased towards females (i.e. k becomes smaller), (4) the male care period, R_m, increases and (5) the female refractory period, R_f, decreases. Thus, filial cannibalism is facilitated by conditions 1–5 (Fig. 1b–f).

When the number of clutches males rear in a breeding cycle, C, increases, the search time, s_m^*, becomes longer ($\partial s_m^*/\partial C > 0$) because more females become unreceptive. However, this condition does not always inhibit filial cannibalism (Fig. 2). Equation (7) makes $\partial p^*/\partial C = -(\partial Q/\partial C)/(\partial Q/\partial p^*) = -\{1 + (\partial Q/\partial s_m^*)\ (\partial s_m^*/\partial C)\}/(\partial Q/\partial p^*) = -\{1 - (R_m/s_m^{*2})\ (\partial s_m^*/\partial C)\}/(\partial Q/\partial p^*)$. Noting that $\partial Q/\partial p^* < 0$, it follows that the equilibrium number of cannibalized clutches can either increase or decrease with increasing C depending on the sign of $\{1 - (R_m/s_m^{*2})\ (\partial s_m^*/\partial C)\}$. Specifically, it increases with increasing C if the magnitude of increase in s_m^* by C is sufficiently low (to hold that $(\partial s_m^*/\partial C)/s_m^* < s_m^*/R_m$), while it decreases if the increase in s_m^* by C is sufficiently high (to hold that $(\partial s_m^*/\partial C)/s_m^* > s_m^*/R_m$).

These results are obtained analytically, and therefore not changed qualitatively by parameter values. In addition, the shape of $w(E)$ does not change the qualitative result as long as it holds that $w(0) = 0$ (indicating that the male reproductive gain is zero if the male has no energy reserves), $w'(E) > 0$ (the male reproductive gain increases with increasing energy reserves), $w''(E) < 0$ (the male reproductive gain saturates), $\lim_{E \to \infty} w(E) = 1$ (the male reproductive gain has an upper limit).

DISCUSSION

The model has revealed that two primary factors can influence the occurrence of filial cannibalism by parental males. One concerns an intrinsic factor (parent's own energy status), while the other concerns extrinsic factors associated with the breeding system, including mate search efficiency, population density, sex ratio and parental time expenditure by both sexes. These two factors operate on filial cannibalism through different mechanisms.

The first mechanism influences filial cannibalism by changing the relative value of eggs as an energy reserve. Parental males with lower energy reserves, E_0 (i.e. poor physical condition) benefit more from filial cannibalism because they would more efficiently improve their brooding ability or survival by consuming eggs (as indicated by the saturating curve of the function $w(E)$: $d(w'/w)/dE < 0$).
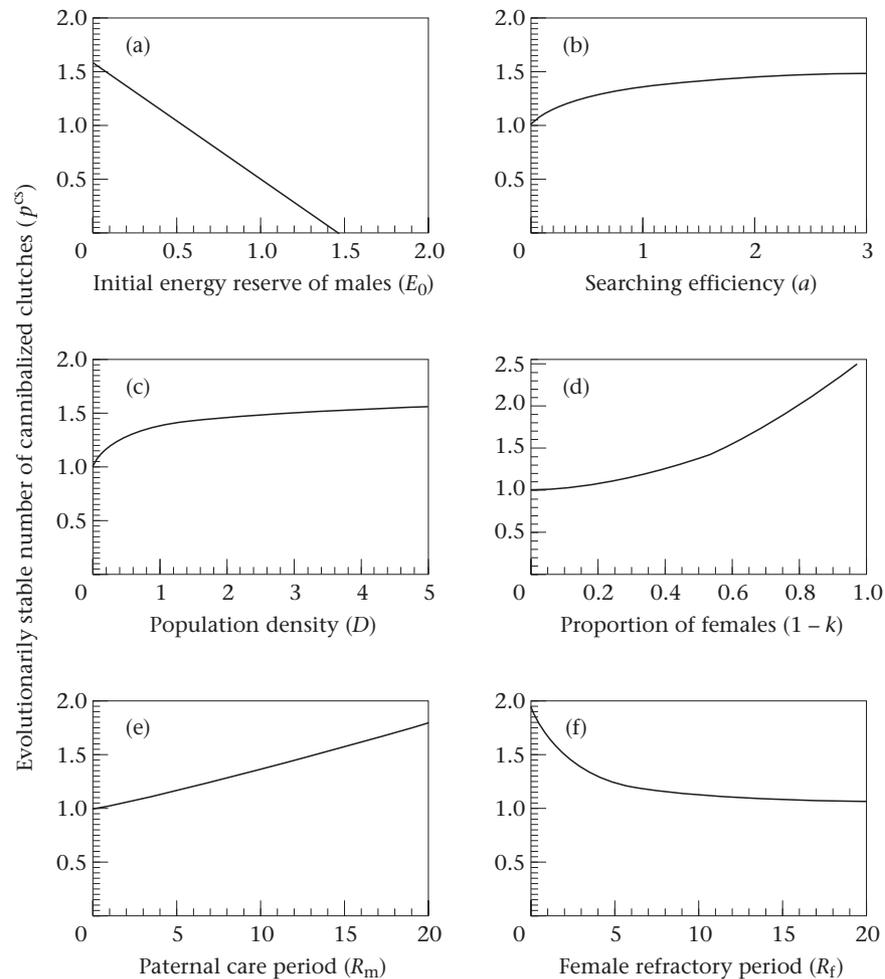
Figure 1. Examples of the effect of each parameter on the optimal number of clutches cannibalized in a breeding cycle (p^{cs}). (a) Initial parental energy reserves (E_0), (b) mate search efficiency (a), (c) population density (D), (d) sex ratio (proportion of females ($1-k$)), (e) male care period (R_m), (f) female refractory period (R_f). These results are not changed qualitatively by parameters as proved in the text. The parameters used in this figure are (a, D, k, R_m, R_f, E_0, e, C)=(1, 2, 0.5, 10, 3, 0.2, 1, 5), where k is the proportion of males, e is the energy conversion efficiency and C is the number of clutches. A concrete function, $w(E)=E/(E+0.3)$, is used, where E is the energy reserve and $w(E)$ the male's reproductive gain.

Thus filial cannibalism (p^{cs}) is predicted to increase as parental energy reserve (E_0) decreases. This prediction was first presented by Rohwer (1978), and has been supported by a dynamic programming model (Sargent 1992; Sargent et al. 1995) and numerical simulations (Lindström 2000). In many fish with paternal care, filial cannibalism frequently occurs when parental physical condition is lowered (DeMartini 1987; Belles-Isles & FitzGerald 1991; Marconato et al. 1993; Okuda & Yanagisawa 1996a; Lindström 1998). Although some of these studies merely showed a correlation between filial cannibalism and male condition at the population level, there seems to be no doubt that parental energy reserve is one of the most important factors influencing filial cannibalism in nature.

The second mechanism facilitates filial cannibalism through an increase in mate availability, which is caused by high efficiency of mate search, high population density, female-biased sex ratio, long male care period and short female refractory period. Increased mate availability reduces the time ($s_m^\star$) required to acquire receptive females, and allows males to remate quickly. This reduces

the value of present offspring relative to increased future reproduction, and increases filial cannibalism.

The result that parental time expenditure by males (R_m) influences filial cannibalism has an interesting implication for the evolution of filial cannibalism as the parental strategy. In our model, an increase in male parental expenditure led to an increased incidence of filial cannibalism. This seems to be counterintuitive because parental care and filial cannibalism have opposite effects on the survival of current offspring: the former increases offspring survival but the latter decreases it. However, this apparent paradox is resolved by considering the effect of male parental expenditure on mate availability. When males invest more in parental care, they increase their opportunities to exploit any surplus of female investment, by which they can compensate for the energetic cost of parental care. The prediction that filial cannibalism increases with increasing paternal care can be derived from different theoretical approaches. Extensive parental care may lower the physical condition of males or increase their mortality (Knapton 1984); filial cannibalism
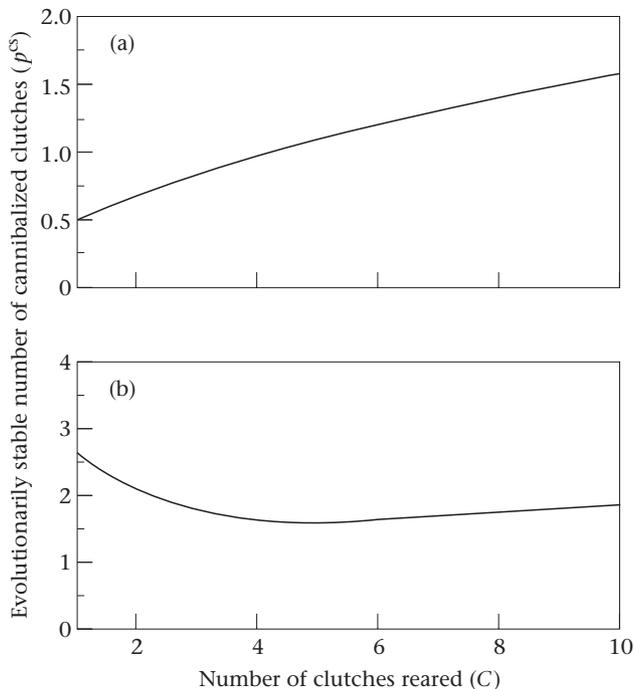
Figure 2. The effect of the number (C) of clutches on the equilibrium number of clutches cannibalized (p^{cs}). Filial cannibalism can increase or decrease with increasing clutch number (C). The number of cannibalized clutches monotonously increases with increasing C in (a), while it is minimized at the intermediate clutch number in (b). The parameters used in this figure are (a, k, R_m, R_f, E_0, e)=(1, 0.5, 10, 3, 0.2, 1). A function, $w(E)=E/(E+0.3)$, is used. (a) $D=2$, (b) $D=200$. See Fig. 1 legend for definitions of parameters.

will then be facilitated by the depletion of male energy reserves (Sargent 1992; Sargent et al. 1995) or by the female-biased sex ratio, as predicted in the present model. Unfortunately, there are no empirical data to test the prediction that the relative amount of parental expenditure by the two sexes can influence filial cannibalism. However, this prediction is easily testable. In fish, for example, water temperature and food availability affect the male care period and female refractory period differently (Kvarnemo 1994, 1997; Ahnesjö 1995). Such factors often vary to a great extent between populations at different latitudes, or seasonally within a population. It would be worth looking at intraspecific variation in filial cannibalism rates in relation to these factors.

Our model shows that there is no consistent relationship between the number of clutches a male rears in a breeding cycle (i.e. collateral investment, C; sensu Parker & Simmons 1996) and filial cannibalism (Fig. 2). This is well explained by considering two countering effects of collateral investment on filial cannibalism. An increase in collateral investment by males, which decreases their mate availability (Parker & Simmons 1996), has a potential to inhibit filial cannibalism. On the other hand, it also decreases the value of one clutch relative to the remaining clutches, inciting males to filial cannibalism. The model analysis has shown that whether filial cannibalism increases or decreases with increasing collateral investment depends on the relative strength of these two

opposite forces. Indeed previous models (Sargent 1992; Sargent et al. 1995) showing a positive effect of clutch number on partial filial cannibalism have not considered the effect of collateral investment through mate availability. The countering effects of clutch number on filial cannibalism may explain why it sometimes increases with increasing clutch number (DeMartini 1987; Kraak 1996; Ito & Yanagisawa 2000), but not in all cases (Petersen & Hess 1991; Lindström & Sargent 1997; Kvarnemo et al. 1998; Svensson et al. 1998). More careful examination of detailed data is needed to test the prediction of the effect of collateral investment on filial cannibalism.

This is the first model that has attempted to demonstrate the importance of breeding system components as well as parental condition in determining filial cannibalism. However, the results are obtained at the sacrifice of some reality in population dynamics such as inter-subpopulation immigration or stochasticity, although the majority of key factors considered as essential determinants of mate availability have been incorporated. To give further insight into how filial cannibalism evolves in nature, the present model needs to be extended accordingly. In many animals with paternal care, females preferentially mate with males with better energy status to ensure that their partner will be a good parent (Andersson 1994). Females may also prefer males that already have some eggs to reduce the risk of filial cannibalism, as reported for some fish (Unger & Sargent 1988; Knapp & Sargent 1989; Kraak & Groothuis 1994; but see Jamieson & Colgan 1989). Although we have not incorporated female mate choice into the present model, to keep it analytically tractable, the result that filial cannibalism increases with increasing mate availability suggests a potential influence of female mate choice on male filial cannibalism. In general female choosiness generates an asymmetric distribution in mate availability among males, and this would therefore generate a variance in the male's tendency to filial cannibalism. In some cases it may drive further evolution of female mate preferences to lower the risk of filial cannibalism. To examine the outcome of such male–female coevolutionary processes, however, we need to extend the present model to incorporate the female's mate choice explicitly (see Lindström 2000). Another possible and important extension is to consider a case where 'bourgeois and parasitic' males coexist in a population (Taborsky 1998). In fish, males that gain little access to mates often perform sneaking behaviour (i.e. exploit access to mates by attempting to fertilize female gametes monopolized by 'bourgeois' males; Taborsky 1994). Since such behaviour would lower the value of clutches by decreasing the paternity of the caring male, parental males (i.e. bourgeois males) may adjust the proportion of eggs to be cannibalized according to the vulnerability to sneaking (Maekawa & Hino 1987). There have been few empirical studies relating the occurrence of filial cannibalism to the breeding system components (Okuda 1999, 2000). The predictions of the present paper now need to be tested by comparative methods or experiment, such as density or sex ratio manipulation.

Acknowledgments

References

Abrams, P. A., Harada, Y. & Matsuda, H. 1993. On the relationship between quantitative genetic and ESS models. *Evolution*, **47**, 982–985.

Ahnesjö, I. 1995. Temperature affects male and female potential reproductive rates differently in the sex-role reversed pipefish, *Syngnathus typhle*. *Behavioral Ecology*, **6**, 229–233.

Alonzo, S. H. & Warner, R. R. 1999. A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success. *Behavioral Ecology*, **10**, 105–111.

Alonzo, S. H. & Warner, R. R. 2000. Dynamic games and field experiments examining intra- and intersexual conflict: explaining counterintuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*. *Behavioral Ecology*, **11**, 56–70.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Balshine-Earn, S. & Earn, D. J. D. 1997. An evolutionary model of parental care in St. Peter's fish. *Journal of Theoretical Biology*, **184**, 423–431.

Belles-Isles, J.-C. & FitzGerald, G. J. 1991. Filial cannibalism in sticklebacks: a reproductive management strategy? *Ethology, Ecology and Evolution*, **3**, 49–62.

Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.

DeMartini, E. E. 1987. Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). *Animal Behaviour*, **35**, 1145–1158.

Dominey, W. J. & Blumer, L. S. 1984. Cannibalism of early life stages in fishes. In: *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by G. Hausfater & S. B. Hrdy), pp. 43–64. New York: Aldine.

Elgar, M. A. & Crespi, B. J. 1992. *Cannibalism: Ecology and Evolution Among Diverse Taxa*. Oxford: Oxford University Press.

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

FitzGerald, G. J. 1992. Filial cannibalism in fishes: why do parents eat their offspring? *Trends in Ecology and Evolution*, **7**, 7–10.

FitzGerald, G. J. & Whoriskey, F. G. 1992. Empirical studies of cannibalism in fish. In: *Cannibalism: Ecology and Evolution Among Diverse Taxa* (Ed. by M. A. Elgar & B. J. Crespi), pp. 238–255. Oxford: Oxford University Press.

Hausfater, G. & Hrdy, S. B. 1984. *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine.

Ito, S. & Yanagisawa, Y. 2000. Mate choice and cannibalism in a natural population of a stream goby, Rhinogobius sp. *Ichthyological Research*, **47**, 51–58.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences II. The 'handicap' principle. *Evolution*, **45**, 1431–1442.

Jamieson, I. G. & Colgan, P. W. 1989. Eggs in the nests of males and their effect on mate choice in the three-spined stickleback. *Animal Behaviour*, **38**, 859–865.

Knapp, R. A. & Sargent, R. C. 1989. Egg-mimicry as a mating strategy in the fantail darter, *Etheostoma flabellare*: females prefer males with eggs. *Behavioural Ecology and Sociobiology*, **25**, 321–326.

Knapton, R. W. 1984. Parental investment: the problem of currency. *Canadian Journal of Zoology*, **62**, 2673–2674.

Kondoh, M. 2001. Co-evolution of nuptial gift and female multiple mating resulting in diverse breeding systems. *Evolutionary Ecology Research*, **3**, 75–89.

Kraak, S. B. M. 1996. Female preference and filial cannibalism in *Aidablennius sphynx* (Teleostei, Blenniidae); a combined field and laboratory study. *Behavioural Processes*, **36**, 85–98.

Kraak, S. B. M. & Groothuis, T. G. G. 1994. Female preference for nests with eggs is based on the presence of the eggs themselves. *Behaviour*, **131**, 189–206.

Kvarnemo, C. 1994. Temperature differentially affects male and female reproductive rates in the sand goby: consequences for operational sex ratio. *Proceedings of the Royal Society of London, series B*, **256**, 151–156.

Kvarnemo, C. 1997. Food affects the potential reproductive rates of sand goby females but not of males. *Behavioral Ecology*, **8**, 605–611.

Kvarnemo, C. 1998. Why male cannibalism won't cause a female-biased OSR: a comment on Smith and Wootton's paper. *Reviews in Fish Biology and Fisheries*, **8**, 93–98.

Kvarnemo, C., Svensson, O. & Forsgren, E. 1998. Parental behaviour in relation to food availability in the common goby. *Animal Bahaviour*, **56**, 1285–1290.

Lindström, K. 1998. Effects of costs and benefits of brood care on filial cannibalism in the sand goby. *Behavioral Ecology and Sociobiology*, **42**, 101–106.

Lindström, K. 2000. The evolution of filial cannibalism and female mate choice strategies as resolutions to sexual conflict in fishes. *Evolution*, **54**, 617–627.

Lindström, K. & Sargent, R. C. 1997. Food access, brood size and filial cannibalism in the fantail darter, *Etheostoma flabellare*. *Behavioral Ecology and Sociobiology*, **40**, 107–110.

Maekawa, K. & Hino, T. 1987. Effect of cannibalism on alternative life histories in charr. *Evolution*, **41**, 1120–1123.

Marconato, A., Bisazza, A. & Fabris, M. 1993. The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). *Behavioral Ecology and Sociobiology*, **32**, 229–237.

Okuda, N. 1999. Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. *Animal Behaviour*, **58**, 273–279.

Okuda, N. 2000. Interspecific differences in male cannibalistic behavior between two sympatric cardinalfishes (Pisces: Apogonidae). *Journal of Ethology*, **18**, 5–10.

Okuda, N. & Yanagisawa, Y. 1996a. Filial cannibalism by mouth-brooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environmental Biology of Fishes*, **45**, 397–404.

Okuda, N. & Yanagisawa, Y. 1996b. Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behaviour*, **52**, 307–314.

Parker, G. A. & Simmons, L. W. 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society of London, Series B*, **263**, 315–321.

Petersen, C. W. & Hess, H. C. 1991. The adaptive significance of spawning synchronization in the Caribbean damselfish *Stegastes dorsopunicans* (Poey). *Journal of Experimental Marine Biology and Ecology*, **151**, 155–167.

Reynolds, J. D. 1996. Animal breeding systems. *Trends in Ecology and Evolution*, **11**, 68–72.

Rohwer, S. 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist*, **112**, 429–440.

Sargent, R. C. 1992. Ecology of filial cannibalism in fish: theoretical perspectives. In: *Cannibalism: Ecology and Evolution Among Diverse*

Taxa (Ed. by M. A. Elgar & B. J. Crespi), pp. 38–62. Oxford: Oxford University Press.

Sargent, R. C., Crowley, P. H., Huang, C., Lauer, M., Neergaard, D. & Schmoetzer, L. 1995. A dynamic program for male parental care in fishes: brood cycling and filial cannibalism. *Behaviour*, **132**, 1059–1078.

Smith, C. & Wootton, R. J. 1995. The effect of brood cannibalism on the operational sex ratio in parental teleost fishes. *Reviews in Fish Biology and Fisheries*, **5**, 372–376.

Svensson, O., Magnhagen, C., Forsgren, E. & Kvarnemo, C. 1998. Parental behaviour in relation to the occurrence of sneaking in the common goby. *Animal Behaviour*, **56**, 175–179.

Székely, T., Webb, J. N. & Cuthill, I. C. 1996. Mating patterns, sexual selection and parental care: an integrative approach. In: *Vertebrate Mating Systems* (Ed. by M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 159–183. London: World Science Press.

Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M. 2000. An evolutionary approach to offspring desertion in birds. In: *Current Ornithology* (Ed. by V. Nolan Jr & E. D. Ketterson), pp. 271–331. London: Plenum.

Taborsky, M. 1994. Sneakers, satellites and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, **23**, 1–100.

Taborsky, M. 1998. Sperm competition in fish: 'bourgeois' males and parasitic spawning. *Trends in Ecology and Evolution*, **13**, 222–227.

Unger, L. M. & Sargent, R. C. 1988. Allopaternal care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. *Behavioral Ecology and Sociobiology*, **23**, 27–32.

Yamamura, N. & Tsuji, N. 1993. Parental care as a game. *Journal of Evolutionary Biology*, **6**, 103–127.

Appendix 1

The analysis of the reproductive dynamics

The left-hand side of equation (4) is a decreasing function of F_s^* from $(1-k)\,D$ to negative values and the right-hand side is an increasing function of F_s^* from 0, implying that a unique F_s^* and thus a corresponding value of M_s^* exists as a solution. (We confirmed that this system always approaches the stationary values of F_s^* and M_s^*, by conducting numerical calculations under different conditions.) Subsequently, the value of s_m^* ($=1/(a\,F_s^*)$) must be determined uniquely for any given parameter set.

Here we prove that s_m^* is a decreasing function of k. By setting $s_m^*=1/(a\,F_s^*)$, equation (3) can be rewritten as $(1-k)-\{1/(aD\,s_m^*)\}=k\,R_f/[s_m^*+\{R_m/(p^*+C)\}]$. Consider a set of parameters that gives a solution of s_m^*. Suppose that s_m^* does not increase with increasing k. With increasing k, the right-hand side of this equation increases, while the left-hand side, which is a decreasing function of s_m^*, decreases. Then it follows that this equation never holds for the increased k, implying that any s_m^* cannot be a solution of this equation. This contradicts the fact that a unique solution of s_m^* exists for any parameter set. Thus, s_m^* should decrease with increasing k. By following the same logic, it can be determined that s_m^* is an increasing function of p^* and R_f, and a decreasing function of a, D and R_m.

Appendix 2

The analysis of the evolutionary dynamics

Equation (6) is rewritten as $dp^*/dt=g[w'(E)/w(E)-s_m^*/\{(C+p^*)s_m^*+R_m\}]$. Setting the right-hand of this equation to zero, it holds that $w'/w=s_m^*/\{(C+p^*)s_m^*+R_m\}$. This can be rewritten as $w/w'=\{(C+p^*)\,s_m^*+R_m\}/s_m^*$, suggesting that if and only if $dp^*/dt=0$, then it holds that $Q=(C+p^*)+(R_m/s_m)-(w/w')=0$. Furthermore, Q should be positive and negative if and only if dp^*/dt is positive and negative, respectively.