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SIGNALLING, MATING SUCCESS AND PATERNAL INVESTMENT IN STICKLEBACKS (GASTEROSTEUS ACULEATUS): A THEORETICAL MODEL

by

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(With 5 Figures)
(Acc. 10-VII-1995)

Summary

I present an optimisation model that links paternal investment, male display and female choice. Although deviced for sticklebacks, it readily applies to other fish with male guarding behaviour. It relies on a few basic assumptions on the ways hatching success depends on paternal investment and clutch size, and male survival on paternal investment and signaling. Paternal investment is here a state-dependent decision, and signal a condition-dependent handicap by which males inform females of how much they are willing to invest. Series of predictions are derived on female and male breeding strategies, including optimal levels of signaling and paternal investment as functions of clutch size, own condition, and residual reproductive value, as well as alternative strategies such as egg kleptoparasitism. Some predictions already have empirical support, for which the present model provides new interpretations. Other might readily be tested, *e.g.* by simple clutch-size manipulations.

Introduction

One proposed function for secondary sexual characters is that of enhancing breeding success by attracting potential mates. Mate choice is a widespread feature of mating systems. The benefits of choosiness may be direct (*e.g.* high-quality partners are better in rearing common offspring) or indirect (high-quality partners transmit 'better' genes, in terms of viability or attractiveness, to the common offspring) (KIRKPATRICK & RYAN, 1991). The former provides a more plausible explanation to mate choice whenever partners show important levels of parental investment.

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Such is the case in sticklebacks (*Gasterosteus aculeatus*): females are the choosy sex, and males have long been known for their conspicuous secondary sexual characters (courtship behaviour, breeding coloration, *etc*), as well as for their high level of paternal investment (*e.g.* WOOTTON, 1976). The latter consists mainly in building the nest, defending it against predators (often conspecific males), and providing oxygen to the eggs through a characteristic fanning behaviour. Fanning may be the most demanding part of parental care in terms of time and energy; during the breeding season, males can spend up to two thirds of their time just fanning eggs (VAN IERSEL, 1953).

The quality of paternal care thus certainly depends on male condition. It is under natural-selection pressure since hatching success depends on it; furthermore, sexual selection is also at work insofar as females prefer good fathers (HEYWOOD, 1989; PRICE *et al.*, 1993; SCHLUTER & PRICE, 1993). But, in order to choose, females must detect the ability of potential mates to care for youngs, which in turn leads to a selection for males to signal their willingness to care. Signals, however, may be costly, and thereby affect male condition and ability to care. All this raises a number of questions regarding the determinants and consequences of paternal investment and signaling. How does paternal investment depend on male condition? How does it correlate with signaling? How does it affect hatching and mating success? Such questions have both empirical and theoretical (evolutionary) aspects.

Several models have been recently devoted to the evolution of signaling (*e.g.* ANDERSSON, 1982; POMIANKOWSKI,1988; GRAFEN, 1990; HEYWOOD, 1989; PRICE *et al.*, 1993). These models were developed in the context of the controversy about the validity of the handicap-theory of mate choice (ZAHAVI, 1975). Since their main purpose was to investigate whether (and how) male traits can evolve as honest signals of quality, such models were given explicit genetic bases.

The present model has a different purpose: it does not investigate an evolutionary process, but assumes evolutionary equilibrium. Accordingly there will be no genetics in it: all individuals are supposed to bear the same genotype, which is the one allowing to take the optimal decision as a function of local circumstances. Indeed, differences among males in paternal investment do not need to be heritable (*e.g.* ZAHAVI, 1977; MOTRO, 1982; HEYWOOD, 1989; HOELZER, 1989); they may simply result from state-dependent decisions, that differ because state and/or local conditions differ. Similarly, the variance in signal level may be purely condition-dependent (*sensu* MAYNARD-SMITH, 1985; *e.g.* DOMINEY, 1983; NUR & HASSON, 1984).

There is strong empirical justification in sticklebacks (see below) that both signaling and paternal investment depend largely on environmental conditions and own state, which itself varies with environmental hazards such as parasitisation (*e.g.* MILINSKI & BAKKER, 1990). An important question is whether the observed plasticity is adaptive. One way to investigate this question is to derive optimal reaction norms for paternal investment and signaling, then to compare results with empirical data. The purpose of the present model is precisely to derive such specific predictions, to compare expected patterns with published work on stickleback behaviour, and to suggest further experimental tests on relevant points.

Assumptions.

The primary function of paternal investment (Ip) is to increase offspring survival (p_o). This has been empirically demonstrated in a number of fish with paternal care, including sticklebacks (VAN DEN ASSEM, 1967), fathead minnows (SARGENT, 1988) and rock bass (SABAT, 1994). So let us assume a positive relationship between these two variables (Fig. 1a). A convex shape seems realistic; a unit increase in fanning activity should have the strongest effect when average fanning level is low.

Paternal investment also has costs, both in terms of risk and energy spent, which potentially decrease the father's survival (p_a) (Fig.1a). A convex shape again seems realistic; when fanning activity is already high, any increase must be taken over the time necessary for feeding and the energy necessary for maintenance. These assumptions of convexity ensure that the optimal solution is not boundary, which would result in either absence of paternal investment, or maximal investment followed by death. A mathematical formulation of these assumptions is provided in Appendix A, together with a numerical example.

A third assumption concerns egg number. The more clutches in a nest, the more oxygen is needed to ensure a given level of offspring survival. In other words, for a fixed level of fanning activity, hatching success (p_o) should decrease as the number of eggs in the nest (Nm) increases. VAN

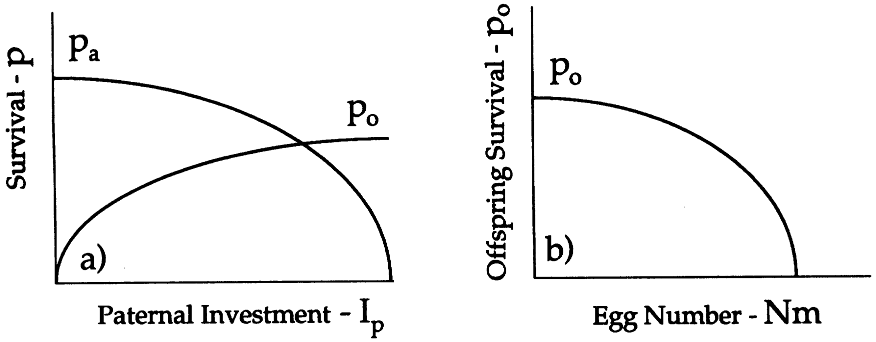

Fig. 1. a) Male survival (p_a) is assumed to decrease with his level of paternal investment (Ip), while offspring survival (p_o) increases with paternal investment and b) decreases with egg number (Nm). For reasons explained in the text, these relationships are assumed convex (*i.e.* second-order derivatives are negative).

IERSEL (1953) and ROHWER (1978) similarly assumed that oxygen supply might limit the male's brood size. This relationship is illustrated in Fig 1b, where convexity is assumed again for simple physical reasons: the eggs that require fanning are not those at the periphery of a clutch (who benefit from direct access to oxygen-rich water) but those situated deep in the clutch, where oxygen is quickly depleted. Due to surface-volume relationships, the proportion of eggs that require fanning increases with clutch size, so that the amount of fanning necessary to maintain a given level of hatching success increases more than proportionally.

These two opposing effects of paternal investment (Ip) and egg number (Nm) on offspring survival can be plotted on a single graph in the Ip-Nm plane, where p_o is represented by isoclines of increasing value as Ip increases and as Nm decreases (Fig. 2a). The slope of isoclines is derived in Appendix B, and illustrated by a numerical example.

Fitness.

At any age, the optimal allocation decision is that which maximizes current reproductive value v_t. This can be written:

$$\text{Max } v_t = p_o Nm + p_a v_{t+1} \tag{1}$$

where Nm is fecundity for the current breeding cycle (total number of eggs in a male's nest), p_o is hatching success, p_a is adult survival until the next breeding cycle, and v_{t+1} its reproductive value at the start of next

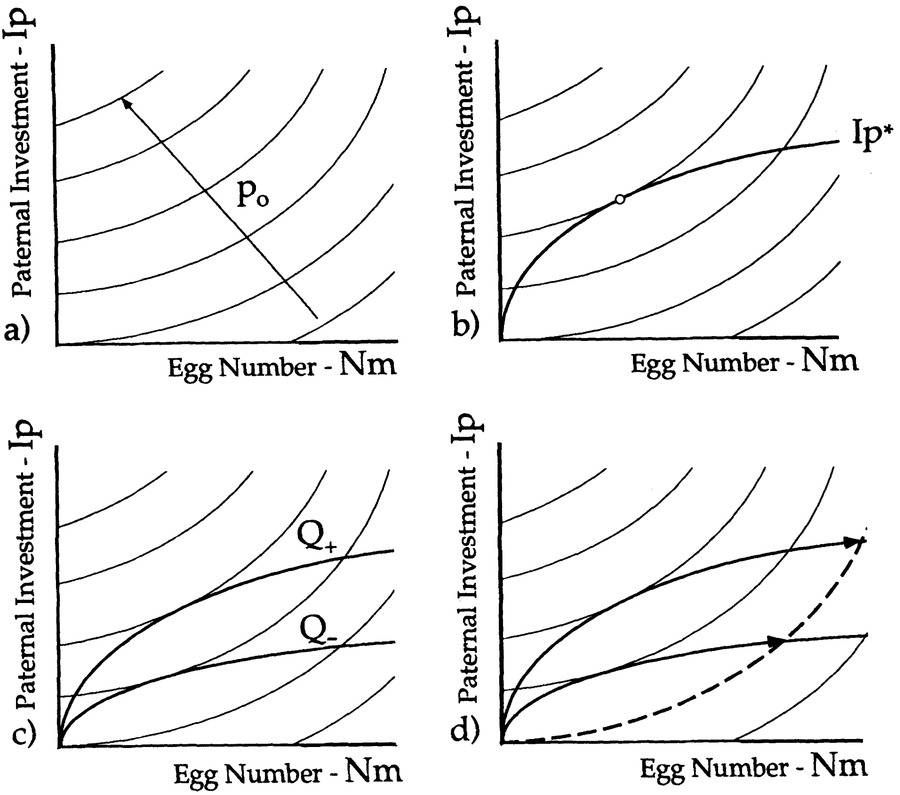

Fig. 2. a) The assumptions about the way offspring survival depends on paternal investment and egg number (Fig. 1) determine p_0-isoclines (curves) in the Ip-Nm plane. Offspring survival increases (arrow) as Ip increases and as Nm decreases. b) The optimal paternal investment level (Ip*) increases with egg number (Nm) in such a way that offspring survival first increases, then decreases with egg number. Offspring survival is maximal where the Ip* curve is tangent to a p_0-isocline (circle). c) High-quality males (Q+) are expected to provide a higher optimal level of paternal investment, such that the associated offspring survival is also better for any Nm value. d) Females are expected to lay (arrows) in the male's nest that provides the highest p_0 value available. As a result, at equilibrium all males should lie on the same p_0-isocline (dashed curve).

breeding cycle. This equation (1) is equivalent to the classical statement (Williams, 1966) that organisms should maximise the sum of current reproduction and residual reproductive value. It readily applies to males, where Nm is the product of the number of females attracted (N), times their fecundity (m, number of eggs per female). For females, this equation is simplified: when entering the breeding sites, a female has a fixed number of eggs (m) to lay and simply wants to provide them with the highest hatching success by choosing a good father. Since the choice actually made does not imply any change in her own reproductive effort, it is not bound to affect her future survival. Thus, for females, (1) is reduced to

$$\text{Max } p_o \qquad (2)$$

From comparison of equations (1) and (2), the differences in the objectives of the two sexes are straightforward. As opposed to females, males do not necessarily want to maximise current hatching success, and this creates a potential for conflict.

Strategies.

Female strategy, aimed at maximising hatching success, consists of visiting males and inspecting them for cues as to potential p_o (including male signal level – see below). Males lying on a high p_o-isocline (Fig. 2a), *i.e.* with few eggs in the nest but ready to spend a high level of paternal investment, should be preferred. Female search is assumed to bear no special cost, which is realistic insofar as males concentrate in one breeding site. If females have to visit several breeding sites far apart, search may bear some costs (MILINSKI & BAKKER, 1992). Their consequences on the predictions from the present model will be discussed later.

Male strategy is twofold. They may first adjust their level of paternal investment to local conditions. The optimal level depends on the way Ip affects the two components of reproductive value; that is, both current reproduction p_oNm and residual reproductive value p_av_{t+1} (Eqn.1). These relationships are illustrated on Fig. 3a. Their shapes depend on external as well as internal conditions, which therefore affect the optimal value. The second aspect of male strategy concerns mating success: they may try to attract females by displaying their willingness to care for offspring, and thereby convince them to spawn. Let us now address these two strategies in turn.

Optimal paternal investment.

The problem is represented graphically in Fig. 3a. Since natural selection maximises the sum of the two fitness components (Eqn.1), the optimal Ip

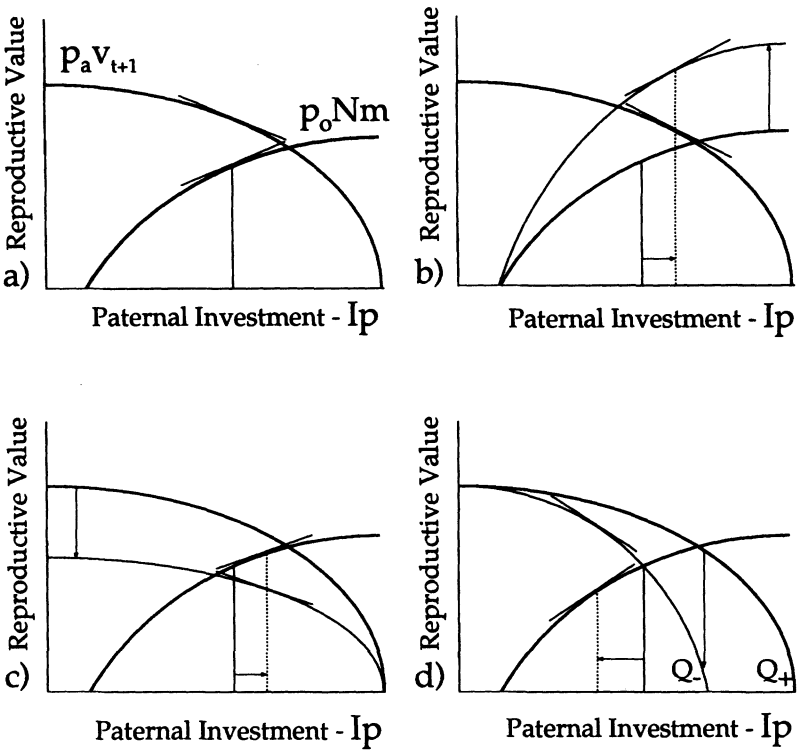

Fig. 3. a) The two components of male's reproductive value are affected by its level of paternal investment. His effective fecundity (p_oNm) increases, while his residual reproductive success (p_av_{t+1}) decreases. The optimal investment level is noted with a vertical line. b) As egg number in nest increases, the optimal level of paternal investment also increases. c) As residual reproductive value decreases, the optimal investment increases. d) The optimal paternal investment of low-quality males (Q-) is lower than that of high-quality ones (Q+).

is determined by the point where the slopes of the two curves have the same absolute value.

Egg number.

As shown in Fig. 3b, an increase in Nm results in a steeper slope of the p_oNm curve, so that the optimal paternal investment value shifts to the right. This is understandable intuitively; if for some reason a male succeeds in getting many clutches, a slight increase in paternal investment will make a lot of increase in present reproductive success, but only at slight cost in residual reproductive value. This prediction has empirical support as well; fanning activity has been shown to increase with egg numbers in sticklebacks (VAN IERSEL, 1953) as well as in other fish with paternal care such as bluegill sunfish (COLEMAN *et al.*, 1985), fathead minnow (SARGENT, 1988), or the blenny *Aidablennius sphynx* (KRAAK & VIDELER, 1991). A mathematical formulation and a numerical example are provided in Appendix C. Fig. 2b illustrates in the Ip-Nm plane how the optimal paternal investment increases with egg number. As can be seen, Ip* first increases rapidly with Nm, then levels off. As a result, hatching success first increases with Nm, because the negative effect of egg number is overcompensated by the simultaneous adjustment of Ip. A maximum in p_o is then reached (where the Ip* curve is tangent to a p_o isocline, open circle), after which p_o declines. For females, this decline implies a net decrease in fitness. In males however, as argued above, hatching success is not the only component of fitness; male reproductive value may increase with egg number even though survival chance per egg decreases, because an absolute greater number of eggs hatch. Thus, males should keep on accepting new females even though hatching success decreases as eggs are added to their nests.

Residual reproductive value.

A side result of optimizing Ip is the negative effect of residual reproductive value on optimal paternal investment, as evident in equation (C2) and illustrated in Fig. 3c. For a given number of eggs, males should increase their investment throughout the season, because their residual reproductive value decreases with time. This result was also reached by SARGENT & GROSS (1993) and will not be commented further here.

Male condition.

A result more relevant to the present study (because we are interested in female choice for paternal investment) concerns the way Ip* may change with male condition or quality (Q). Quality is defined here by its positive effect on survival under bad conditions. On this definition, low-quality males suffer more when increasing paternal investment. A mathematical formulation of this is provided in Appendix D, and illustrated in Fig. 3d. As can be seen, residual reproductive value decreases more rapidly with paternal investment in low-quality males. Since the slope of $p_a v_{t+1}$ is steeper at any Ip value, the equilibrium condition shifts to the left. As a result, the optimal paternal investment (for a given egg number) correlates with quality. A numerical example is developed in Appendix D, and illustrated in the Ip-Nm plane (Fig. 2c)

Dynamics of clutch laying

The dynamics of clutch laying of females in a population can be illustrated in the Ip-Nm plane (Fig. 2d). Let us assume for the moment that females can detect both male quality and egg number (by inspecting male display and visiting nest - see below), and therefrom infer Ip and p_o. The highest-quality male should be chosen by the first females, since he provides the highest marginal increase in p_o. As a result, the associated p_o will first increase up to a maximal value, then decline. Further females should however keep on choosing this male, as long as he provides the highest available p_o value; that is, until this value has declined down to the level offered by other males (dashed p_o-isocline in Fig. 2d). At this point, females should switch to the 2nd-highest male. The associated p_o value will thus first increase, then decline back to the common value. This process will continue until all males have received eggs, and lie along the common p_o-isocline (dashed in Fig. 2d). At this point, all nests provide the same return to females, so that additional clutches will be distributed among all males, but in such a way that their hatching success decrease at the same rate. When the process stops, all males lie on the same p_o-isocline, but of course their Nm differ, and correlate with quality. The equilibrium relationship between egg number and male quality is derived in Appendix E (together with a numerical example), and illustrated in Fig. 4a. The important point is that, if females can assess male quality, then at equilibrium high-quality males have more eggs in their nests.

This dynamics and equilibrium result from the same logic that underlies the 'polygyny-threshold model' (*e.g.* VERNER & WILLSON, 1966; ORIANS, 1969), according to which female breeding birds may accept polygyny when its disadvantages (shared help from the male) are overcompensated by strong differences in male and/or territory quality. Although originally developed for birds, this concept readily applies to fish. The only difference here is that, as a consequence of our assumptions, polygyny is actually beneficial to females over the lower part of the egg-number range (*i.e.* up to the maximum in p_o, open circle in Fig. 2b).

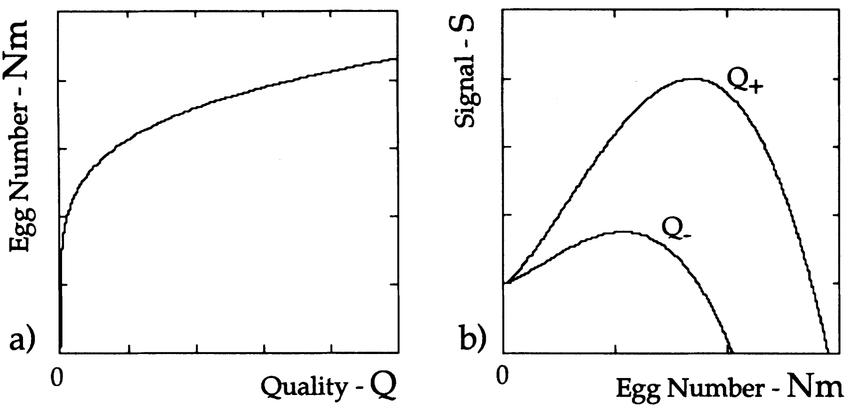

Fig. 4. a) At equilibrium, egg number in a nest increases with male quality (Q). b) As males receive more eggs, they should first increase, then decrease their signal level. For any egg number, the optimal signal level is higher in high-quality males (Q+).

It follows from the same logic that, at equilibrium, female clutches are ideally-free distributed with respect to hatching success. This conclusion of course relies on the same assumptions that underlie the ideal-free distribution in foraging theory (*e.g.* FRETWELL & LUCAS, 1970; FRETWELL, 1972), namely that females are free to move from male to male, and can perfectly assess both male quality and egg number. Any cost to female search, as well as errors in the information-gathering process, would cause departures from this distribution. As a result, the correlation between egg number and male quality would decrease, and hatching success would show positive correlations with both egg-number and male quality.

Optimal signaling

Let's turn now to the second part of male strategy, that of attracting females. As pointed above, males differ in the level of paternal investment they are willing to pay, due to differences in either quality or residual reproductive value. A male which is ready to invest above average should signal it to females. The reason appears clearly from the last paragraph on the dynamics of clutch laying. For a fixed egg number, the higher the investment, the higher the resulting p_o, which is exactly what females are looking for. Females should thus prefer males ready to invest more, and this in turn further increases male fitness through enhanced mating success. Male advertisement is thus under pressure from sexual selection, or perhaps preferably, signal selection (ZAHAVI, 1981).

The theory of signal states that, whenever there is a conflict of interest between the sender and receiver of a message (as is the case here), the signal must be costly to be reliable (the so-called 'handicap' principle; ZAHAVI, 1975; GRAFEN, 1990). Otherwise, low-quality males would signal as much as high-quality ones, and thus get as many eggs. Females should not trust a signal which is not costly, because it is too easy to cheat for the male. By contrast, a costly signal can be reliable: costs prevent cheating, insofar as high-quality males can also afford the costs of a higher signal level.

Possible signals may involve coloration, behaviour, morphology (*e.g.* fin length; T.C.M BAKKER & B. MUNDWILER, unpublished data) and nest quality. All such signals have potential costs. Those of coloration may be direct (increased probability of predation) or indirect, since carotenoids are needed otherwise for the immune system (refs in LOZANO, 1994; WEDEKIND, 1994). Such signals differ in plasticity. The one referred to in this model would be very plastic (*e.g.* coloration or behaviour), and so could track changes in residual reproductive value, quality, and egg number.

Its optimal level, S*, can be calculated as a function of the above variables (v_{t+1}, Q, Nm), while taking into account that males also adjust Ip* to these same variables. Derivations are given in Appendix F, together with a numerical example. Fig. 4b presents graphically changes in S* with quality and egg number. As can be seen, the optimal signal level first increases, then decreases with egg number. This arises because signaling expresses the marginal gain of additional eggs, which first increases, then decreases with egg number.

The egg number for which the signal vanishes corresponds to the point where fitness gains (in terms of increased offspring number) are overcompensated by fitness costs (in terms of decreased offspring and adult survival). At this point males do not signal anymore, and further eggs are refused. This maximal egg number is higher for good-quality males, as is in fact the overall signal value for any given Nm. This arises from the fact that high-quality males are ready to invest more for a given egg number, and therefore signal more.

A general consequence of such relationships between signaling, egg number and quality is that combined information on both Nm and S* allow females to gain precise ideas, both of the amount of paternal investment a male is ready to spend, and of the associated p_0. It is worth noting that S* alone would not suffice: males expressing a given signal value may be either low-quality ones with few eggs, or high-quality ones with many eggs (Fig. 4b). Therefore, checking egg number in the nest usefully completes the information.

Predictions and tests

Several variables involved in the system under study, together with their interconnections, are presented in a path diagram in Fig. 5. Some of the qualitative predictions from the model appear on this graph. Several already have empirical support.

First, consider female behaviour. Empirical evidence exists that females are more attracted by brighter males (MILINSKI & BAKKER, 1990, 1992; BAKKER & MILINSKI, 1991; BAKKER, 1993; BAKKER & MUNDWILER, 1994). But, as also expected from the present model, they inspect egg number in the nest as well before taking a decision (BELLES-ISLES *et al.*, 1990; GOLDSCHMIDT *et al.*, 1993). Furthermore, nests with a few eggs are preferred overempty ones (RIDLEY & RECHTEN, 1981; JAMIESON & COLGAN, 1989; BELLES-ISLES *et al.*, 1990; GOLDSCHMIDT *et al.*, 1993). According to the present model, this should occur even when females perceive no difference in male quality. It is worth noting that the explanation offered by the present model for this behaviour differs from the classical 'copying' (GOLDSCHMIDT *et al.*, 1993). Based on the result that hatching success is expected to increase with egg number over the lower part of the range (*i.e.* up to the open circle in Fig. 2b), this explanation might be tested by checking the hatching success over an experimentally manipulated range of egg numbers.

The special dynamics of clutch laying expected from the present model (*i.e.* that nests are filled first successively, then simultaneously; Fig. 2d) would also need further empirical investigations.

A second set of predictions concerns signaling, and also already has empirical support. One is that signal level first increases, then decreases with egg number (Fig. 4b). It has indeed been observed that male coloration brightens (JAMIESON & COLGAN, 1989; GOLDSCHMIDT *et al.*, 1992) and

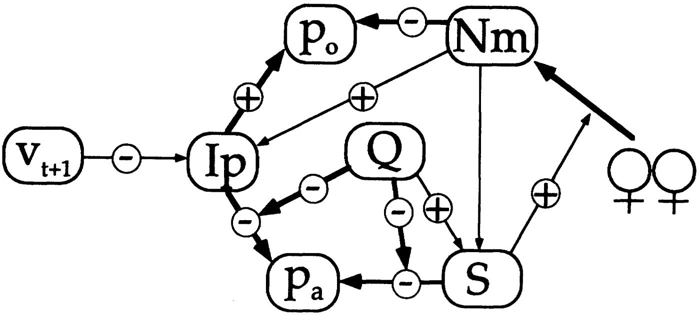

Fig. 5. Path diagram of the relationships assumed (thick arrows) or predicted (thin arrows) between components of the model. Further explanations in the text.

that males display more (VAN IERSEL, 1953; SEVENSTER-BOL, 1962; SEGAAR *et al.*, 1983; 'T HART, 1985; SEGAAR & DE BRUIN, 1985; JAMIESON & COLGAN, 1989) after the acquisition of the first clutch of eggs. Display level then decreases as clutch number further increases, and stops after the male has a certain number of clutches (VAN IERSEL, 1953). KRAAK & VIDELER (1991) also observed that display in male blennies *Aidablennius sphynx* depends on egg number, and in particular decreases above some value (Fig. 4b). The maximal brood size (above which males stop display and refuse further eggs) varies strongly among males, which KRAAK & VIDELER (1991) attribute to differences in maximum fanning capacity, certainly a component of male quality.

There is also evidence from sticklebacks that male quality affects signaling, mating success and paternal investment. Males in better body condition are brighter (MILINSKI & BAKKER, 1990; FRISCHKNECHT, 1993; BAKKER & MUNDWILER, 1994), they get more eggs (BAKKER & MUNDWILER, 1994) and display a higher paternal investment in terms of fanning activity (WOOTTON, 1994).

Furthermore, as already noted, fanning activity increases with egg number (VAN IERSEL, 1953). It is worth noting that both observational and experimental data should in this case show a positive relationship, but with different shapes. Observational data should follow equation (B1) (slope of the p_o-isocline; e.g. dashed line in Fig. 2d), while experimental data should meet condition (C1) (*e.g.* Ip* curves on Fig. 2b to d).

Although hatching success (p_o) depends on both paternal investment and egg number, at equilibrium no such correlation should exist, because of the ideal free distribution of clutches. Thus, experimental data should reveal a negative effect of egg number and a positive effect of paternal investment on hatching success. Experimentally increasing egg number (clutch size manipulations), for instance, should lower hatching success. By contrast, observational data should show an equal hatching success for all males in a population. As pointed above, however, this prediction relies on the assumptions that females pay no costs when searching males, and make no errors when gathering information. Departure from these assumptions might result in a weak positive correlation between egg number and hatching success, such as observed in fathead minnows by SARGENT (pers. comm.) in non-manipulated conditions.

The precise value of this hatching success depends on how many clutches in total are to be spread among available males, and therefore on female fecundity and sex-ratio. With a low average number of clutches per nest, males will stay on a higher p_o-isocline: hatching success will be high, contrasting with a low average level of paternal investment. Signaling, on the other hand, will be high. Empirical data suggest indeed that under conditions of female shortage and increased male-male exploitative competition, the average signal level increases (T.C.M. BAKKER & B. MUNDWILER, unpublished data). It is worth noting however that such an increase might also arise from interactive competition, insofar as signals might also act to deter neighbours. Modelling interactive competition, however, would be a game problem in itself, and beyond the scope of the present model.

For very low female availability, the dynamics of clutch laying predicts that some males will remain without eggs. This implies a bimodal distribution of egg numbers, with two categories of males, some getting many eggs, and others none. This further increases the scope for sexual selection and the overal level of signaling.

An interesting alternative male strategy arises in such a case, namely egg kleptoparasitism. Indeed, low-ranking males are at risk of getting no eggs at all. If they can manage to get just a few, they will automatically move on a higher p_o-isocline. This should suffice to make females lay here rather than in empty nests, even those of higher-quality males. To be precise, males should not care for stolen eggs; but the point is that visiting females ignore eggs' provenance, and are thus fooled when infering p_o. As a result, a small difference at the beginning may be enough to start a kind of runaway process, ending in a breeding success higher than expected from quality alone. This may explain the empirical observation of egg kleptoparasitism by males (VAN DEN ASSEM, 1967; LI & OWINGS, 1978; GOLDSCHMIDT *et al.*, 1992; MORI, this volume). Here again, the explanation provided for this behaviour by the present model differs from the classical one, which relies on female copying.

As a conclusion, the present model seems to offer parsimonious explanations for the results of empirical observations and experiments on the reproductive biology of sticklebacks, in particular with respect to signaling and paternal behaviour. It thereby offers new insights and/or alternative interpretations for the ultimate causes of some aspects of this behaviour (*e.g.* female preference for non-empty nests and egg kleptoparasitism in males). Several of the model's assumptions and predictions already have good empirical support; its validity might be further checked by testing some other predictions, *e.g.* by simple clutch-size manipulations. It is worth noting that this model also appears readily applicable to other fish species presenting a similar male guarding behaviour (*e.g.* the blenny *Aidablennius sphynx* mentioned above).

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Appendix A: Assumptions on offspring and adult survival

The first- and second-order assumptions about hatching success (p_o) are:

$$\frac{\partial p_o}{\partial Ip}>0, \quad \frac{\partial^2 p_o}{\partial Ip^2}<0 \tag{A1}$$

and

$$\frac{\partial p_o}{\partial Nm}<0, \quad \frac{\partial^2 p_o}{\partial Nm^2}<0 \tag{A2}$$

while those about adult survival (p_a):

$$\frac{\partial p_a}{\partial Ip}<0, \quad \frac{\partial^2 p_a}{\partial Ip^2}<0 \tag{A3}$$

Examples of relationships that meet these assumptions are:

$$p_o = cIp^{.5} - b\,Nm^2 \tag{A4}$$

$$p_a = d - e\,Ip^2 \tag{A5}$$

Appendix B: Slope of the p_o-isoclines

By definition, the positive effect of Ip (A1) and the negative effect of Nm (A2) exactly cancel out on the p_o-isoclines, so that

$$\frac{dIp}{dNm} = -\frac{\partial p_o/\partial Nm}{\partial p_o/\partial Ip}. \tag{B1}$$

This equation expresses how much paternal investment should be increased to exactly compensate for a unit increase in egg number in terms of hatching success. Using (A4) as an example, this gives:

$$\frac{dIp}{dNm} = \frac{4b}{c} NmIp^{.5} \tag{B2}$$

Thus, large egg number and high paternal investment result in steep isoclines (Fig. 2).

Appendix C: Optimal paternal investment

The first-order condition for a maximum in reproductive value (v) is that its derivative with respect to paternal investment vanishes:

$$\frac{dv}{dIp} = Nm\frac{\partial p_o}{\partial Ip} + v_{t+1}\frac{\partial p_a}{\partial Ip} = 0 \tag{C1}$$

from which the optimal value (Ip*) can be sought. Using the numerical examples (A4) and (A5):

$$Ip^* = \left(\frac{cNm}{4e\ v_{t+1}}\right)^{2/3} \tag{C2}$$

Appendix D: Effect of quality

Quality (Q) is defined by its positive effect on survival under bad conditions. More specifically, paternal investment induces a lower mortality in high-quality individuals. Formally:

$$\frac{\partial\left({}^{\partial p_a}\!/_{\partial Ip}\right)}{\partial Q} > 0 \tag{D1}$$

Thus, the higher Q, the shallower $\partial p_a/\partial Ip$. As a result, and given the convexity of p_o on Ip (A1), condition (C1) is met at higher Ip value (Fig. 3d). If we assume for example that the parameter *e* in (A5) depends on Q in the following way:

$$e = {}^{1}\!/_{Q} \tag{D2}$$

then $\partial p_a/\partial Ip = -2Ip/Q$, from which it can be checked that condition (D1) is met. Substituting (D2) in (C2) gives the dependence of Ip* on Q:

$$Ip^* = \left(\frac{cNmQ}{4\ v_{t+1}}\right)^{2/3} \tag{D3}$$

Appendix E: Q-Nm relationship

At equilibrium, females lay in such a way that the p_o equalize among nests. High-quality males are able to provide higher p_o values for a given Nm, which induces a positive correlation between Q and Nm. This relation is derived by substituting (D3) in (A4):

$$Q = \frac{4v_{t+1}(p_o + bNm^2)^3}{c^4Nm} \tag{E1}$$

Note that p_o is here a constant, the actual value of which depends on the local situation (see 'dynamics of clutch laying'). Equation (E1) expresses a positive relationship between quality and egg number, which is illustrated in Fig. 4a, where v_{t+1}, p_o, b and c are fixed to some arbitrary values. As can be seen, the number of eggs in a nest at equilibrium increases with male quality, first rapidly, then more slowly.

Appendix F: Optimal signaling

Signaling is assumed to have a negative effect on adult survival:

$$p_a = p_a(Ip, Q, S), \quad \partial p_a / \partial S < 0 \tag{F1}$$

Its optimal value maximizes the male reproductive value. The first-order condition for such a maximum is:

$$\frac{dv}{dS} = \frac{\partial v}{\partial p_a}\frac{dp_a}{dS} + \frac{\partial v}{\partial p_o}\frac{dp_o}{dS} + \frac{\partial v}{\partial Nm}\frac{dNm}{dS} = 0 \tag{F2a}$$

where

$$\frac{\partial v}{\partial p_a}\frac{dp_a}{dS} = v_{t+1}\left(\frac{\partial p_a}{\partial S} + \frac{\partial p_a}{\partial Ip}\frac{\partial Ip}{\partial Nm}\frac{dNm}{dS}\right), \tag{F2b}$$

$$\frac{\partial v}{\partial p_o}\frac{dp_o}{dS} = Nm\frac{dNm}{dS}\left(\frac{\partial p_o}{\partial Nm} + \frac{\partial Ip}{\partial Nm}\frac{dp_o}{dIp}\right), \tag{F2c}$$

and

$$\frac{\partial v}{\partial Nm}\frac{dNm}{dS} = p_o\frac{dNm}{dS} \tag{F2d}$$

The expressions for p_a (F1) and p_o (e.g., A4) can be substituted in (F2), from which S* can be found as a function of Q, Nm, v_{t+1} and Ip:

$$S^* = S^*(Nm, Q, Ip, v_{t+1}) \tag{F3}$$

Furthermore, males adjust their level of paternal investment to Q, Nm, and v_{t+1}. Ip* (e.g. D3) can be substituted in (F3), thus allowing to drop the dependence of S* on Ip.

Numerical example.

To account for the effect of signaling on adult survival (F1), we add a term to (A5):

$$p_a = d - Ip^2/Q - fS \tag{F4}$$

Thus (F2) becomes:

$$\frac{dNm}{dS} = \frac{fv_{1+1}}{p_o - 2bNm^2} \tag{F5}$$

Introducing (D3) into (A4), then the resulting equation into (F5) (in order to account for the dependence of p_o on Nm), we obtain:

$$\frac{dS}{dNm} = \frac{c\left(\frac{cNmQ}{4v_{t+1}}\right)^{1/3} - 3bNm^2}{fv_{t+1}} \tag{F6}$$

which has for solution:

$$S^* = \frac{Nm}{4fv_{t+1}}(3p_o - bNm^2) + C \tag{F7}$$

where C is an integration constant. The dependence of S* on Q is given by substituting (A4) and (D3) in (F7). This relationship is illustrated in Fig. 4b, with arbitrary values for f, v_{t+1}, b and C.