

# Parental care and predation risk in fish

Carin Magnhagen

*Magnhagen, C., Swedish University of Agricultural Sciences, Department of Aquaculture, S-901 83 Umeå, Sweden*

*Received 2 March 1992, accepted 25 May 1992*

When caring for offspring several factors influence an animal's decision concerning how much risk to take. The value of the offspring and the parent's probability of future reproduction are, among others, two main determinants of risk-taking, and there is often a trade-off between the two. Here I discuss how predator avoidance influences the outcome of the conflict between parental care and the individual's own survival, using examples from reproducing fish. Factors discussed are offspring age, number and vulnerability, and age of the parent, in relation to the amount of risks taken in order to maximize fitness.

## 1. Introduction

Both predation on, and predator avoidance by, a reproducing animal may be important costs of reproduction (Bell & Koufopanou 1986, Stearns 1989), so that the predation risk experienced by reproducing animals is worthy of more consideration in future research. Reproductive behaviour often makes an animal more susceptible to predation (see reviews by Lima & Dill (1990) Magnhagen (1991) and Ylönen et al. (1992)), either when using conspicuous displays to attract partners or when defending offspring. Clearly, risks taken during current reproductive events can completely eliminate the possibility of future reproduction, and thus trade-offs between current and future reproductive investments, as well as between a number of behavioural alternatives in the animal's current situation, have to be made.

Parental investment was defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring". The question of how much to invest (including taking risks of being taken by a predator) in parental care has been much debated in life history theory (e.g. Clark & Ydenberg 1990, Sargent & Gross 1985, 1986, Curio 1987, Coleman & Gross 1991, see also Clutton-Brock 1991). The goal of animals should be to maximize lifetime reproductive success, but the way in which they evaluate how to optimize parental behaviour has been a controversial issue. Two important factors influencing parental investment are the value of the current brood and the future reproductive potential of the parent (Williams 1966), as well as the relation between the two. Trivers (1972) argued

that animals should behave in such a way that past investments would not be wasted. This concept was later called the “Concorde fallacy” by Dawkins (1976) who argued that an animal should not base its decisions on past efforts but instead on expected future benefits. In some cases individuals may be able to assess their expected future reproduction directly, for example, by estimating the frequency of potential partners, which was found to determine mate desertion rate in the biparental cichlid, *Herotilapia multispinosa*. In this case, there was an increasing probability of males deserting their mates with the increasing availability of females and thus expectations of future reproduction (Keenleyside 1983). However, future benefits often depend on past investments and animals may only be able to assess future expectations based on their past investments (Sargent & Gross 1985). Animals have been found to “commit the Concorde fallacy” in many studies (Weatherhead 1979, 1982, Coleman et al. 1985); the tactic is often adaptive (Curio 1987) and coherent with life history theory. The concept of a fallacy, therefore, has been heavily criticized and said to be misleading (Coleman & Gross 1991, but see also Jokela & Vuorisalo 1992, Coleman & Gross 1992).

Much of the focus on this topic thus far has been on birds (reviewed by Montgomerie & Weatherhead 1988). In this paper I will review some factors that have been shown to be important for decision-making in reproducing fish, in connection with predation risk on individuals engaging in parental care. Ecological differences between birds and fish, such as survival and growth patterns, may lead to different predictions in the two taxa. My aim with this paper is to point out what factors to take into account when studying risk-taking in fish during the parental phase, to mention some factors that can be either confounding or give opposite predictions, and to give some examples of studies made on this topic.

In fishes, about 80% of all families exhibit no parental care (Blumer 1979, Sargent & Gross 1986). Instead they rely on other strategies to maximize their reproductive output. Compared with terrestrial vertebrates fish often specialize in quantity rather than quality of the progeny they produce (Wootton 1990). Some fish protect their eggs by hiding them, for example, in gravel

or vegetation, without guarding, whereas others have evolved elaborate techniques of nest building and caring for their offspring. For fish with parental care, trade-offs between defence and predator avoidance must commonly occur. Often both egg predators and piscivores are abundant and the conflicts are obvious. Predation on nest guarding fish is probably high compared to, for example, birds (A. P. Møller pers. comm., but see Björklund 1990), which makes fish suitable for this kind of study. In studies cited in this review the predator is either a threat to the parent only, or to both parent and offspring. Predation risk of the offspring only is mentioned in a few examples, but in those cases as well an increase in defence led to an increased mortality risk of the parent due to aggressive interactions with the approaching predator.

## 2. Factors influencing response towards predators in fish with parental care

### 2.1. Reproductive status of the parent

When fish are reproducing they go through different behavioural stages, such as nest building, courting, spawning, and guarding, and should have different incentives for risk-taking during these phases. It may seem evident that individuals without any offspring should do everything to avoid being preyed upon, but it might be important to defend a territory or a nest in order to be able to reproduce in the future. This will lead to trade-offs between different types of behavioural patterns as early as in the pre-reproductive phase. Male three-spined sticklebacks, *Gasterosteus aculeatus*, exhibited a higher degree of boldness towards a predator when they had a brood of young compared to those individuals that had just built a nest, who in their turn were bolder than non-reproducing individuals (Huntingford 1976). Similarly, in pumpkinseed sunfish, *Lepomis gibbosus*, changes in aggressive responsiveness towards a predator dummy were found over the reproductive phase (Colgan & Gross 1977), with an increase in approach and bite frequencies when going from nesting through spawning to brooding, followed by a decrease in these types of behaviour when vacating the nest.

## 2.2. Clutch size

A large clutch has, of course, a higher fitness value to its parents than a smaller clutch, and risk-taking should be positively correlated with clutch size. Smallmouth bass, *Micropterus dolomieu*, increased their defence of offspring against a predator when their broods were experimentally augmented and vice versa in the case of reduced broods (Ridgway 1989). Similarly, female Central American cichlids, *Aequidens coeruleopunctatus*, guarding their offspring, stayed away longer from their brood after being scared away if the brood had been experimentally reduced, and came back faster if the brood was increased (Carlisle 1985). Whether or not the parent fish will invest more in a naturally larger brood may, however, depend on a higher investment in the past (see below), since brood size and past investment are likely to be correlated. Coleman et al. (1985) teased these two effects apart by reducing broods in the bluegill sunfish, *Lepomis macrochirus*, at different stages of the nest guarding phase. These authors were able to demonstrate that the intensity of defence in the males towards egg predators was correlated with both past investment and brood size.

## 2.3. Offspring age

Under predation pressure, risk-taking should increase with time already spent with a particular brood, not because investments already made should not be wasted [as discussed by Trivers (1972) and in connection with the "Concorde Fallacy" (Dawkins 1976)], but because of the increased probability of offspring survival with offspring age, and also because of a decrease in future chances of reproduction for the parent. Both these factors give the current brood a higher value with age (Montgomerie & Weatherhead 1988). Three-spined sticklebacks changed their behaviour with both the age of the eggs and the number of eggs in their nest (Pressley 1981). When presented with a dummy predator, males that remained near the nest and even attacked the predator had older eggs and/or a larger number of eggs than individuals that deserted their nest. The time for a male to return to his nest after

deserting was negatively correlated with the age of the eggs (Pressley 1981). Also in the common goby, *Pomatoschistus microps*, after having been scared away by a predator, egg guarding males returned faster to their nests as the eggs developed (Magnhagen & Vestergaard 1991). By coming back faster they accepted a higher risk of being eaten, simulated by an enclosed predator placed outside the nest opening. This increase in risk-taking probably reflects the increased value of the brood with age. These gobies also increased risk-taking with parental age. The males came back to the nest just as fast in the presence of a predator as in its absence at the end of the season, which was not the case at the beginning of the season. Having only one breeding season, the probability of future reproduction thus had an effect on the amount of risk-taking these males were prepared to accept (also discussed below). In contrast, the value of offspring hatched late in the season can be lower than offspring hatched earlier because of a lower probability of late-hatching fry to reach maturity in time for the oncoming breeding season, or by having a lower reproductive success due to small size. This was the explanation offered for a decrease in risk-taking observed in nest guarding sticklebacks at the end of the season (Ukegbu & Huntingford 1988).

## 2.4. Future reproductive opportunities

Whether animals really increase risk-taking during reproduction with increasing age (and consequently with a decrease in future reproductive opportunities) is under debate (Reid 1988). What seems to be an increase in reproductive effort may simply be an increase in experience and skill. In fish, growth is indeterminate, and thus older parents are also larger, and perhaps less vulnerable to predation. In the black goby, *Gobius niger*, young individuals refrained from spawning in the presence of a predator, while older individuals kept on reproducing in the same situation (Magnhagen 1990). This result was interpreted as higher risk-taking by the older individuals due to their lower future reproductive opportunities. However, even though the older individuals were found to be eaten by predators (cod, *Gadus morhua*)

of the size used in this study, vulnerability between age classes (and thus size) probably differed and could also influence the outcome of the experiments. Curio (1988) predicted that the delay of maximum parental effort was to be expected only in relatively long-lived species, that is, species with a high ratio between average life span and maximal life span. For animals to increase risk-taking with a decrease in future reproductive opportunities one would expect an age-dependent mortality rate, and also that the animals are able to assess their own age. One potential cue may be the degree of senescence (Curio 1988), but this is so far virtually unknown.

### 2.5. Offspring vulnerability

The vulnerability of the offspring should be important for risk-taking by the parent, with the highest risks taken when the offspring are in their most vulnerable stages. In sticklebacks, the defence of a brood increases as the eggs approach hatching (Huntingford 1977 and above). However, after hatching a decrease in defence was found as the fry approached independence (Huntingford 1977). A decrease in defence as offspring become less vulnerable may also depend on a reduced capability to improve their survival (Sargent & Gross 1986, Ridgway 1988). For example, in smallmouth bass, *Micropterus dolomieu*, males showed an increase in defence as their brood developed from egg to wriggler and fry, followed by a decrease as the fry "swim-up" from the nest (Ridgway 1988) and become more independent of the parent. They then become more or less impossible to efficiently guard and defend against predators.

### 3. Conclusions

When studying parental care one must realize that the amount of investment and hence risk-taking is not static either within species or within individuals, but varies with both intrinsic and environmental conditions. A dynamic model would therefore be appropriate for predicting levels of risk-taking in a dangerous situation created by a fish caring for offspring (Sargent & Gross 1986,

Clark & Ydenberg 1990). The variables to be included in a model should differ in different systems, but the potential reproductive value of the offspring to the parent should always be considered. The reproductive value of the offspring depends, on the one hand, on the parent's future prospects of reproduction. For this to be evaluated, the age-dependant mortality rate should be known, and also the availability of mates, and perhaps the current body condition of the parent, influenced, for example, by food availability. On the other hand, from the parent's point of view, the offspring's reproductive value depends also on brood size, as well as on their survival probability, which increases with age but should also be influenced by food abundance and predator density. Some factors influencing the value of the offspring can work in opposite directions, which can make predictions of risk-taking difficult. For example, when a decrease in the parent's probability of future reproduction at the end of the breeding season should increase the value of the current brood, the lower probability of survival or maturation of the offspring may instead decrease the value and thus the motivation for taking risks (Ukegbu & Huntingford 1988).

Furthermore, the relative vulnerability of parent and offspring differs both between species and between individuals and is likely to influence anti-predator behaviour. Whether individual differences in vulnerability due, for example, to differences in size or condition, changes decisions of risk-taking has not, to my knowledge, been studied. This should be possible in fish that often show a large variation in those traits. Decisions of risk-taking may differ between species with only one caring parent and those with biparental care, depending on differences in the survival possibilities of offspring in the case of the parent's death. In biparental species the sexes may differ in response to predators. If, for example, females have a higher reproductive cost for producing one clutch of eggs compared to the males' investment in sperm, one would expect females to take higher risks to defend the clutch. In the cichlid *Cichlasoma nigrofasciatum* females always invested more than males when guarding behaviour was studied (Lavery & Keenleyside 1990), and perhaps similar patterns could be detected for risk-taking.

In conclusion, to maximize life-time reproductive success, a combination of the factors mentioned above, relevant to the species and specific environmental conditions, should be considered for the “decision of action” in a reproducing fish encountering a predator. In order to make predictions of behavioural trade-offs and risk-taking these factors should be distinguished for the species studied, for example by finding what limits the fitness of the individuals as discussed by Sih (1992, this volume).

*Acknowledgements.* I thank Ingrid Ahnesjö and Staffan Ulfstrand for valuable comments on this manuscript. I also thank Hannu Ylönen for organising the NCE-course on “Predation stress and behavioural adaptations of prey” and for being invited on this course.

## References

- Bell, G. & Koufopanou, V. 1986: The cost of reproduction. — In: Dawkins, R. & Ridley, M. (eds.), *Oxford surveys in evolutionary biology*: 83–131. Oxford University Press, Oxford.
- Björklund, M. 1990: Nest failures in the scarlet rosefinch *Carpodacus erythrinus*. — *Ibis* 132:613–617.
- Blumer, L. S. 1979: Male parental care in the bony fishes. — *Quart. Rev. Biol.* 54:149–161.
- Carlisle, T. R. 1985: Parental response to brood size in a cichlid fish. — *Anim. Behav.* 33:234–238.
- Clark, C. W. & Ydenberg, R. C. 1990: The risks of parenthood. I. General theory and applications. — *Evol. Ecol.* 4:21–34.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. — Princeton University Press, Princeton.
- Coleman, R. M., Gross, M. R. & Sargent, R. C. 1985: Parental investment decision rules: a test in bluegill sunfish. — *Behav. Ecol. Sociobiol.* 18:59–66.
- Coleman, R. M. & Gross, M. R. 1991: Parental investment theory: the role of past investment. — *Trends Ecol. Evol.* 6:404–406.
- 1992: Reply to Jokela & Vuorisalo. — *Trends Ecol. Evol.* 7:169.
- Colgan, P.W. & Gross, M. R. 1977: Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibbosus*) over the reproductive phase. — *Zeitschr. Tierpsychol.* 43:139–151.
- Curio, E. 1987: Animal decision-making and the ‘Concorde Fallacy’. — *Trends Ecol. Evol.* 2:148–152.
- 1988: Relative realized life span and delayed cost of parental care. — *Amer. Nat.* 131:825–836.
- Dawkins, R. 1976: *The selfish gene*. — Oxford University Press, Oxford.
- Huntingford, F. 1976: A comparison of the responses of sticklebacks in different reproductive conditions towards conspecifics and predators. — *Anim. Behav.* 24:694–697.
- Jokela, J. & Vuorisalo, T. 1992: How to rescue the Concorde Fallacy. — *Trends Ecol. Evol.* 7:169.
- 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.
- Lavery, R. J. & Keenleyside, H. A. 1990: Parental investment of a biparental cichlid fish, *Cichlasoma nigrofasciatum*, in relation to brood size and past investment. — *Anim. Behav.* 40:1128–1137.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. — *Can. J. Zool.* 68:619–640.
- Magnhagen, C. 1990: Reproduction under predation risk in the sand goby, *Pomatoschistus minutus*, and the black goby, *Gobius niger*: the effect of age and longevity. — *Behav. Ecol. Sociobiol.* 26:331–335.
- 1991: Predation risk as a cost of reproduction. — *Trends Ecol. Evol.* 6:183–186.
- Magnhagen, C. & Vestergaard, K. 1991: Risk taking in relation to reproductive investments and future reproductive opportunities; field experiments on nest guarding common gobies, *Pomatoschistus microps*. — *Behav. Ecol.* 2:351–359.
- Montgomerie, R. D. & Weatherhead, P. J. 1988: Risks and rewards of nest defence by parent birds. — *Quart. Rev. Biol.* 63:167–187.
- Pressley, P. H. 1981: Parental effort and the evolution of nest-guarding tactics in the threespine stickleback, *Gasterosteus aculeatus* L. — *Evolution* 35: 282–295.
- Reid, W. V. 1988: Age-specific patterns of reproduction in the glaucous-winged gull: increased effort with age? — *Ecology* 69:1454–1465.
- Ridgway, M. S. 1988: Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieu*). — *Can. J. Zool.* 66:1722–1728.
- 1989: The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieu*). — *Ethology* 80:47–54.
- Sargent, R. C. & Gross, M. R. 1985: Parental investment decision rules and the Concorde fallacy. — *Behav. Ecol. Sociobiol.* 17:43–45.
- 1986: Williams principle: an explanation of parental care in teleost fishes. — In: Pitcher, T. J. (ed.), *The behaviour of teleost fishes*: 275–293. Croom Helm, London.
- Sih, A. 1992: Integrative approaches to the study of predation: general thoughts and a case study on sunfish and salamander larvae. — *Ann. Zool. Fennici* 29:183–198.
- Stearns, S. C. 1989: Trade-offs in life-history evolution. — *Funct. Ecol.* 3:259–268.

- Trivers, R. L. 1972: Parental investment and sexual selection. — In: Campbell, B. (ed.), *Sexual selection and the descent of man*: 13–179. Aldine, Chicago.
- Ukegbu, A. A. & Huntingford, F. A. 1988: Brood value and life expectancy as determinants of parental investment in male three-spined sticklebacks, *Gasterosteus aculeatus*. — *Ethology* 78:72–82.
- Williams, G. C. 1966: Natural selection, costs of reproduction and a refinement of Lack's principle. — *Amer. Nat.* 100:687–690.
- Wootton, R. J. 1990. — *Ecology of teleost fishes*. Chapman and Hall, London.
- Ylönen, H., Jędrzejewska, B., Jędrzejewski, W. & Heikkilä, J. 1992: Antipredatory behaviour in *Clethrionomys voles* – 'David and Goliath' arms race. — *Ann. Zool. Fennici* 29:207–216.