

The eggspots of cichlids: Evolution through sensory exploitation?

Die Eiflecken bei Cichliden: Evolution durch Nutzung der Sinne?

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Summary: Many cichlid species independently evolved mouthbreeding as a highly specialised brood care behavior. Egg dummies, resembling the ova of the corresponding species, formed of various parts of the body can be found in different lineages of mouthbreeding cichlids. Most abundant are eggspots, which are conspicuously yellow spots developed on the anal fin of males. Eggspots were believed to have evolved to deceive the females during spawning, thus maximising the fertilisation rates of the males, but empirical studies showed that the presence of eggspots has no effect on fertilisation rates. However, eggspots seem to play a role during mate choice of females. Here, the role of sexual selection in the evolution of eggspots is reviewed and eggspots are hypothesised to have evolved through sensory exploitation. The sensory exploitation hypothesis can explain the shortcomings of previously suggested hypotheses on the evolutionary origin of eggspots.

Key words: egg dummies, natural and sexual selection, sensory exploitation, mimicry, Cichlidae

Zusammenfassung: Bei vielen Cichlidenarten ist Maulbrüten als hoch spezialisierte Brutpflegestrategie mehrmals unabhängig von einander entstanden. Eiattrappen, die den Eiern der dazugehörigen Art ähneln, werden aus oder an verschiedenen Körperteilen gebildet und sind bei verschiedenen Linien maulbrütender Cichliden zu finden. Am häufigsten sind auffällige gelbe Flecken auf den Anales der Männchen zu finden, die als Eiflecken bekannt sind. Lange Zeit nahm man an, dass Eiflecken entstanden sind, um die Weibchen während des Ablaichens zu täuschen und die Befruchtungsrates der Männchen zu maximieren. Empirische Arbeiten haben allerdings gezeigt, dass dies nicht der Fall ist. Eiflecken spielen allerdings eine Rolle während der Partnerwahl der Weibchen. In dieser Arbeit wird ein Überblick über die Rolle der sexuellen Selektion in der Evolution von Eiflecken gegeben und die Hypothese aufgestellt, dass Eiflecken durch Sinnesausnutzung entstanden sind. Diese Hypothese kann Mängel von früheren Hypothesen zur Evolution von Eiflecken erklären.

Schlüsselwörter: Eiattrappen, natürliche und sexuelle Selektion, Nutzung der Sinne, Mimikry, Cichlidae

1. Introduction

The family Cichlidae is the most species rich vertebrate family (BARLOW 2000, TURNER et al., 2001). All cichlids show complex brood care behaviours, and species of various phylogenetic lineages evolved maternal mouthbreeding as one of the most derived brood care strategies (KEENLEYSIDE 1991). In these maternal mouthbreeders, pair bond formation is usually reduced, so that the two sexes only meet for

spawning. The females pick up the oocytes into their mouths, where they are fertilised, and guard them until the offspring is fully developed (FRYER & ILES 1972).

Some groups of these maternal mouthbreeders show different forms of egg dummies. Egg dummies are morphological structures or colour patterns resembling the ova of the corresponding species. The ova of most maternal mouthbreeders are comparatively large and conspicuously yellow due to the high amount of

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yolk. Egg dummies are usually only developed in the male sex, evolved several times independently in various phylogenetic lineages and are made of different parts of the body.

Since virtually all research has been performed on the eggspots on the anal fin of haplochromine cichlids (a speciose clade of African cichlids; TURNER et al. 2001, SALZBURGER et al. 2005), following implementations are limited on this cichlid group. However, the general mechanisms in the function and evolution of egg dummies in other cichlid groups are supposed to be similar. Except for the haplochromines, eggspots on the anal fin can also be found in species of the genera *Bathybates* and *Callochromis* from Lake Tanganyika, Africa (HERRMANN 1996). Other cichlids have egg dummies made of other parts of the body (tab. 1).

2. Eggspots in haplochromine cichlids

Eggspots are a characteristic trait of haplochromine cichlids (SALZBURGER et al. 2005). According to OLIVER (1984), two different types of eggspots can be distinguished. True eggspots are usually arranged on the anal fin on a longitudinal axis and surrounded by a translucent, unpigmented area, which accentuates the yellow spots. Within the haplochromines, true eggspots can be found in the cichlids of the Lake Victoria region, the mbuna of Lake Malawi, species of the genus *Tropheus* from Lake Tanganyika as well as some river inhabiting clades.

Pseudo-eggspots on the other hand are usually more numerous and continuously distributed on the anal fin. Furthermore, the contrast ring is lacking and pseudo-eggspots are more variable in terms of colour and shape, so that they sometimes hardly resemble the ova. Pseudo-eggspots can be found in the non-mbuna from Lake Malawi and some genera from southern Africa like *Serranochromis* and *Chetia*.

The differentiation between true and pseudo-eggspots is not trivial all the times since a smooth transition exists between the two forms. Some non-mbuna from Lake Malawi (e. g. some *Aulonocara* species) have numerous, continuously distributed spots on the anal fin that sometimes also have a contrast ring. Furthermore, some haplochromines secondarily lost their eggspots (SALZBURGER et al. 2005).

True eggspots are exceedingly well elaborated in pubescent males. In some species, analogous spots can also be found in the posterior part of the dorsal fin. Sometimes, eggspots are developed on the anal fin of females, but they are usually less pronounced and the characteristic contrast ring is lacking.

3. WICKLER's mimicry hypothesis

According to WICKLER (1962b), mouthbreeding lead to an overspecialisation in females. As a consequence of increased egg predation (high conspicuousness of eggs due to the high amounts of yolk) and the risk of being swept

Tab. 1: Egg dummies in cichlids that are not based on pigmentation on the anal fin.

Tab. 1: Eiattrappen bei Cichliden, die nicht auf der Pigmentierung der Analflosse beruhen.

Tribe	Genus	Kind of egg dummy	Reference
Cyprichromini	<i>Cyprichromis</i>	pigmented tip of ventral fin	BÜSCHER (pers. communication), HERRMANN (1996)
Ectodini	<i>Cyathopharynx</i> , <i>Ophthalmotilapia</i>	pigmented lobes at tip of ventral fin	KARINO (1997) HASSENS & SNOEKS (1999)
Tilapiini	<i>Oreochromis</i>	enlarged genital papille	WICKLER (1962b)
Geophagini	<i>Geophagus</i>	knots in the corner of the mouth	SCHMETTKAMP (1998)

away by the current due to the lack of egg adhesion organs, females picked up the oocytes into their mouths before males had a chance to fertilise them. WICKLER (1962b) hypothesised that males with pigmentation on the anal fin that resembles eggs had better fertilisation success because females misidentified those spots as eggs. While females tried to pick up the egg-like spots, males released sperm that fertilised the oocytes within the mouth of females. Thus, selection for the resemblance of spots to eggs lead to the evolution of egg dummies observable in recent cichlids.

In conclusion, eggspots have been proposed as a unique case of intraspecific mimicry (automimicry) where eggspots mimic eggs to influence female's behaviour (WICKLER 1962a). Accordingly, eggspots are thought to have evolved on the male's anal fin to overcome the female's overspecialisation. Eggspots therefore should maximise the fertilisation rates of the males. Furthermore, they might serve as a signal to attract females because males could be observed displaying their eggspots during courtship (WICKLER 1962a, b, 1966).

For several reasons, WICKLER's hypothesis was not undisputed. The resemblance of eggspots to the ova, their role in fertilisation success and the role of natural selection in the evolution of eggspots were questioned.

3.1. Resemblance to the ova

It was criticised that the eggspots of many species do not resemble the corresponding ova in size and/or colour (e. g. AXELROD, 1973, JACKSON & RIBBINK 1975). Although at that time, it was not differentiated between true eggspots and pseudo-eggspots, the question was valid: Are true eggspots really similar in appearance to ova or do observers perceive such similarities due to the subjective perception of humans? The characteristics of the eggspots indeed appear to correspond with those of the ova in most species investigated from Lake Victoria (GOLDSCHMIDT 1991). However, the size of the eggspots often does not match the size of the ova. GOLDSCHMIDT (1991) found a nega-

tive correlation of the eggspot's size and the light intensity in the natural habitat of the species. This size discrepancy is not expected by WICKLER's mimicry hypothesis, since the mimicking eggspots are supposed to look as similar as possible to the eggs.

3.2. Function: fertilisation success and female mate choice

In haplochromines, fertilisation of eggs takes place in the mouth of the females (MROWKA 1987), but experiments showed that fertilisation success of males was independent of the presence and the number of eggspots in *Haplochromis elegans* and *Maylandia aurora* (formerly known as *Pseudotropheus aurora*) (HERT 1989, 1991). Both, males with eggspots and males with experimentally removed spots, had fertilisation rates near a hundred percent. Incidentally, not even the anal fin of the male is necessary for successful fertilisation. Males with amputated anal fins could fertilise eggs successfully during normal spawning (PAULO 1975).

Whereas eggspots do not seem to have a function towards maximising fertilisation success in males, a function of eggspots in courtship behaviour could be documented experimentally. In laboratory as well as in field experiments, females of *Haplochromis elegans* and *Maylandia aurora* preferred males with eggspots and with more spots, respectively (HERT, 1989; HERT, 1991). Female *Maylandia lombardoi* show a preference for one single eggspot as large as possible on the male's anal fin (COULDRIDGE 2002). However, the results are not unequivocal; in *Maylandia zebra* no preference with regard to number or size of eggspots could be found experimentally (HOTTINGER 1987). HOTTINGER (1987) speculated that an optimal number of eggspots might exist in this species.

3.3. Acting of natural selection

Although WICKLER's (1962a, b, 1966) original ideas are plausible, there is one theoretical problem. Because females, especially those of maternal mouthbreeders, invest a lot of energy in

each egg and are therefore limited in the resistance of eggs (RIVERS 1972), they are supposed to be bent on the fertilisation of every single egg. It is hard to imagine that the postulated overspecialisation occurred, because such individuals should be eliminated through natural selection. As a matter of fact, mouthbreeding is not necessarily connected to the presence of egg dummies. In many species, in fluvial as well as in lacustrine habitats, successful oral fertilisation takes place in the absence of egg dummies. This is comprehensible if the strong female drive for egg fertilisation is considered.

4. Alternative hypotheses

The lack of empirical evidence and the theoretical problem of the mimicry hypothesis suggest that alternative approaches for explaining the evolution of eggspots should be considered. The eggspots' attribute of being a secondary sexual character and the importance of eggspots in female choice indicate that eggspots may have evolved through sexual rather than natural selection.

On the one hand, eggspots may serve as a signal in intrasexual selection, like in contests between competing males, indicating the strength or the dominance position of a male (HERT 1989). In *Labeotropheus* sp. from Lake Malawi dominant males have more eggspots (BALON 1977). Furthermore, eggspot numbers correlate with male size in some species (CRAPON DE CAPRONA & FRITZSCH 1984, GOLDSCHMIDT 1991). Dominance position and competitive abilities are often size-dependent (e. g. HOTTINGER 1987, SCHÜTZ & TABORSKY 2005). Thus, eggspots potentially could serve as a signal to assess the competitive abilities of rivals.

Intersexual selection can explain the evolution of secondary sexual characters. Notably, the hypotheses previously proposed in the context of eggspots (see e.g. HERT 1989) suggested that indirect selection maintains the female's mating preference for males with eggspots or males with more eggspots; i.e. the presence of the female's mating preference does not directly affect the female's viability

or fertility but rather her offspring's. Potential benefits for the offspring of a male with well-elaborated eggspots may be (i) an increased fertility if the elaboration of the eggspots and the according female preference are at least partially heritable (FISHER 1930), (ii) an increased viability if eggspots are an honest and costly signal that indicate genetic quality (ZAHAVI 1975), or (iii) an increased resistance to parasites if the elaboration of the eggspots is an indicator for the presence of parasite genes (HAMILTON & ZUK 1982).

Empirical and experimental evidence for or against the mentioned hypotheses on role of intersexual selection in the evolution of eggspots are scarce. Eggspots are mainly built of chromatophores containing carotinoids. Brightness of carotinoid colours depends on diet since carotinoids cannot be synthesised by fish themselves (ENDLER 1983, KODRIC-BROWN 1985). Thus, eggspots could be an indicator of the male's nutritional and/or health status and feeding success because a male with „good genes“ would pick up more carotinoids and become brighter (HERT 1989). Furthermore, in the *Pundamilia nyererei* from Lake Victoria, high colour scores based on carotinoid pigmentation corresponded with low parasite loads indicating that carotinoid based pigmentation may serve as an honest signal of individual quality (MAAN 2006).

5. Evolution through sensory exploitation?

The females' mating preference for well-elaborated eggspots – and thus the presence of eggspots in males – may not be maintained by indirect but direct selection, thus providing direct fitness benefits for the female by increasing her viability or fertility. In haplochromines, males and females meet only for spawning and males obviously do not provide any resources or paternal care (FRYER & ILES, 1972). However, a concept of sexual selection involving direct selection on females' mating preferences that may explain the evolution of haplochromine eggspots is the concept of sensory exploitation in which pleio-

tropic effects play a major role (KIRKPATRICK & RYAN 1991, RYAN 1997).

The female's sensory systems have not only been influenced by selection pressures concerning mate choice. Evolution of sensory systems undoubtedly has been influenced by natural selection (e. g. for food or predator localisation, orientation, etc.). Thus, it is possible that sensory perception in mate choice may be influenced by sensory biases that evolved in other contexts. According to the sensory exploitation hypothesis, males evolve traits to exploit such pre-existing sensory biases or preferences. In this case, the preference of the choosing sex evolved prior to the trait in the other (KIRKPATRICK & RYAN 1991, RYAN 1997). Notably, the females' mating preference for a male with given ornament would not yield in any benefits for the females. The males simply take advantage of the females' sensory system to maximise their reproductive fitness. The female's preference is solely maintained by the benefit it receives in the context in which the sensory bias evolved. Sensory exploitation seems to have played a role in the evolution of secondary sexual characters in túngara frogs (RYAN 1985), water mites (PROCTOR 1991) and fishes of the genus *Xiphophorus* (RYAN & CAUSEY 1989, BASSOLO 1990, 1995, RYAN 1993).

Females of mouthbreeding cichlids undoubtedly evolved sensory capabilities to detect eggs and are supposed to have a strong affinity for them, because they pick them up immediately after spawning. In fact, the ability to detect the eggs directly affects the female's fertility. Every missed egg results in a reduction in fitness, which is especially relevant for haplochromines with their highly reduced fecundity (FRYER & ILES 1972). Consequently, a pre-existing sensory bias might have occurred in early mouthbreeders and might still occur in mouthbreeding species without egg dummies. As a consequence, males would have evolved eggspots in response to this sensory bias. Again, the females' mating preference for a male with well-elaborated eggspots would not yield in any benefits for the females, but the female's preference is solely maintained by the benefit of the detection of eggs after spawning.

The sensory exploitation hypothesis of the eggspot's evolution can account for the discrepancies of WICKLER'S (1966) mimicry hypothesis. As observed, the sensory exploitation hypothesis predicts no other function of the ornament than a role in the female's choice behaviour. Both hypotheses predict structures looking similar to the ova. However, the sensory exploitation hypothesis makes no predictions about the accuracy of the resemblance between ova and eggspots, thus deviant eggspots as observed frequently do not contradict the hypothesis. Furthermore, many eggspots that have minor resemblance with the corresponding ova for human eyes might appear quite similar if perceived with cichlid's sensory abilities in a natural context.

Eggspots have not only the potential advantage of being conspicuous and attractive to females, but also to visually hunting predators (GOLDSCHMIDT 1991). The negative correlation between the eggspots' size and the light intensity in the natural habitat of the species may indicate a disadvantage of having conspicuous eggspots. Eggspots are smaller in clear water with high predation risks than in murkier water (GOLDSCHMIDT 1991). Thus, natural selection for example through predators may modify the outcome of sexually selected traits. In a similar way, natural selection seems to counteract sexual selection in guppies (*Poecilia reticulata*), so that intermediate elaborations of male ornaments can be observed (HOUDE & ENDLER 1990). RYAN et al. (1990) suggested that natural selection might prevent the evolution of favoured traits in a *Xiphophorus* species with a sensory bias.

Certainly it needs to be addressed that the above mentioned mechanisms for the maintenance of female mating preferences for well-elaborated eggspots are not mutually exclusive. Some in fact may act simultaneously or sequentially in the course of a trait's evolution, however, the theoretical basis how these mechanisms may interact are not well understood so far (KIRKPATRICK & RYAN 1991).

To verify the role of sensory exploitation in the evolution of eggspots, the predictions of the hypothesis should be tested experimentally. On

the one hand, mate choice experiments should uncover female preferences for males with eggspots in species in which eggspots are lacking. Methods for examining mate choice in cichlids (e. g. HERT 1989, SEEHAUSEN et al. 1997) as well as for manipulating eggspot presence and number are well established (HERT 1989, COULDRIDGE 2002). Furthermore, advances in the use of video playback techniques might open an array of new possibilities in investigating the role of eggspots in female choice behaviour (ROSENTHAL 1999, OLIVEIRA et al. 2000).

Mate choice experiments should be complemented with phylogenetic analyses to test the hypothesis rigorously. If eggspots really evolved through sensory exploitation, the female preference for males with eggspots is expected to be phylogenetically older than the eggspots. But although our phylogenetic knowledge about East African cichlids is rapidly growing, it is still fragmentary. Because of the large number of species and the wide distribution of haplochromine cichlids throughout Africa, it proved to be difficult to have a representative taxon sampling in phylogenetic analyses. As a consequence, different and sometimes conflicting results were presented in past studies depending on which taxa were included and which gene sequences were analysed (e. g. SEEHAUSEN et al. 2003, VERHEYEN et al. 2003).

6. Conclusions

According to WICKLER (1962b), eggspots evolved to guarantee the fertilisation of the eggs, thus overcoming an overspecialisation of the females. However, empirical and theoretical evidence suggest that other evolutionary mechanisms must be considered to explain the evolution of males' eggspots. Sexual selection theory provides an array of theoretical mechanisms for the evolution of secondary sexual characters.

The evolution of eggspots has never been put into the context of the sensory exploitation hypothesis, although the pre-requisites would be set. A pre-existing sensory bias has likely evolved in females through adaptation of the sensory system to egg detection. Certainly

the different sexual selection hypotheses reviewed herein are not mutually exclusive but some may act simultaneously. However, empirical studies to test the prevailing hypotheses are mostly lacking. Present knowledge about development, function and phylogenetic distribution of eggspots only allow speculations which mechanisms might have played a role.

A better understanding of the evolution of eggspots, and egg dummies in general, would be valuable because in contrast to other mouthbreeding fishes, egg dummies seem to be a common theme of many mouthbreeding African cichlids. Additionally, new insights in mechanisms of the evolution of secondary sexual characters could be gained and broaden our knowledge about sexual selection. Since GOLDSCHMIDT & DE VISSER (1990) ascribed a possible role in speciation processes to the eggspots, further studies in this area might help to understand, how the incredible diversity of cichlids arose in East Africa.

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