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Chemical communication in cichlids: A mini-review

Tina Keller-Costa, Adelino V.M. Canário, Peter C. Hubbard *

Centro de Ciências do Mar, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

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ABSTRACT

The family Cichlidae is well-known for pair-formation, parental care, territoriality, elaborate courtship and social organization. Do cichlids use chemical communication to mediate any of these behaviours? Early studies suggest that parent cichlids can discriminate between conspecific and heterospecific wrigglers (but not eggs) using olfactory cues. Some species are able to discriminate between their own brood and other conspecific broods based on olfaction. The young recognise conspecific adults (although not necessarily their parents) through the odorants they release. In both scenarios, protection of the young from predation is the likely selective force. Some male cichlids use urinary pheromones during courtship and spawning to attract females and induce ovulation. Females – in their turn – may base their mate-choice in part on assessment of those self-same pheromones. The same pheromonal system may be involved in establishing and maintaining the social hierarchies in lek-breeding cichlids. Individual recognition is also mediated by chemical communication. Finally, there is ample behavioural evidence that cichlids – like ostariophysan fish – release alarm cues that alert conspecifics to predation danger. Although the effects of these cues may be similar (e.g., increased shelter use, tighter schooling), they are different substances which remain to be identified. Cichlids, then, use chemical communication associated with many different behaviours. However, given the diversity of cichlids, little is known about the mechanisms of chemical communication or the chemical identity of the cues involved. The aim of this mini-review is to persuade those working with cichlids to consider the involvement of chemical communication, and those working in chemical communication to consider using cichlids.

1. Introduction

Chemical communication is the most ancient and widespread way of exchanging information between organisms. The message is transferred *via* chemicals (semiochemicals) released – actively or passively – to the environment. It may involve only one or a few chemicals or a complex 'bouquet' of different odorants. It can be as specific as a signature which, learnt by the receiver, allows individual recognition. Or it evokes specific and innate responses in conspecifics and, if beneficial to both the sender and receiver, is defined as a pheromone (Karlson and Lüscher, 1959). In fish, studies on chemical communication have focused on reproductive chemicals and alarm cues (Sorensen and Wisenden, 2014); however, there is evidence for its involvement in parent-young interactions, individual-, kin- and conspecific recognition, and territoriality/dominance. Nevertheless, only in a few species have the chemical messengers been identified, and the exact meaning of the messages they convey been deciphered.

Cichlids are excellent models for investigation into chemical communication (Table 1); they show an advanced social structuring and a wide range of behaviours and interactions, including parental care, territoriality and courtship (Baerends and Baerends van Roon, 1950; Barlow, 2000; Keenleyside, 1991). With (currently) 1,662 described species (Fishbase, 2014a), cichlids are the most diverse family in the order Perciformes (perch-like) which, in turn, comprises one third of extant teleosts. Cichlids are divided into four clades, the basal Indian (Etroplinae) and Madagascan (Ptychochrominae) cichlids and the more derived Neotropical (Cichlinae) and African (Pseudocrenilabrinae) cichlids (Sparks and Smith, 2004; Streelman et al., 1998). African cichlids (80% of all cichlids) attract

Abbreviations: 17,20β-P, 17α,20β-dihydroxy-4-pregnen-3-one; 17,20α-P, 17α,20a-dihydroxy-4-pregnen-3-one; 11-KT, 11-ketotestosterone; AVP, arginine-vasopressin; AVT, arginine-vasotocin; EOG, electro-olfactogram; FSH, follicle-stimulating hormone; GnRH, gonadotropin-releasing hormone; GPCRs, G protein-coupled receptors; LH, luteinising hormone; MHC, major histocompatibility complex; OlfC, olfactory receptors related to class C; ORs, olfactory receptors; ORA, olfactory receptors related to class A; TAARs, trace amine-associated receptors; V1Rs, type 1 vomeronasal receptors; V2Rs, type 2 vomeronasal receptors.

* Corresponding author.
E-mail addresses: tkeller@ualg.pt (T. Keller-Costa), acanario@ualg.pt (A.V.M. Canário), phubbard@ualg.pt (P.C. Hubbard).

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a lot of attention because of their explosive speciation and radiation in the East African Rift Lakes (Malawi, Victoria and Tanganyika) at an astonishing (in evolutionary terms) rate; for example, the species radiation in Lake Victoria has occurred over less than 12,400 years since the lake's re-formation after its desiccation in the late Pleistocene (Johnson et al., 1996; Mayer et al., 1998). Each lake has its own unique cichlid flock with an extremely high level of endemicity (99%; Ribbink, 1991). "The value of the cichlid family now equals or has even surpassed that of the Galapagos Darwin's finches" (Baerends, 1991) such that they have become the "darlings of the evolutionary biologists" (Barlow, 2000). Adaptation of the sensory and signalling systems to different environmental conditions has been suggested as an important driver in African cichlid radiation (Seehausen et al., 2008). Focus so far has been on the evolution of colour polymorphism linked to light heterogeneity in the habitat (Seehausen et al., 2008) alongside specialisation for particular trophic niches (Greenwood, 1991). Divergent selection on chemical communication systems may, however, constitute an additional speciation factor; "at least in cichlids, it is likely possible to trace the evolutionary origin and subsequent elaboration of homologous hormonal pheromone systems" (Stacey and Sorensen, 2009). Thus, cichlids offer an exciting opportunity to investigate the possible role of chemical communication as a possible driver of vertebrate speciation. The aim of this short review is to give an overview of the studies on chemical communication systems in this important, diverse fish family, and identify outstanding questions for future research.

2. Parent-young and individual recognition

Parental care in cichlids provides an excellent opportunity to investigate the basis of conspecific recognition; potential parental recognition of their young and, conversely, recognition of parents by the young. Early studies on the jewelfish (*Hemichromis bimaculatus*) showed that egg-care is largely visually mediated; parents do not respond to water conditioned by their eggs but – once hatched – chemicals released by their young induce parental colouration and behaviour, such as 'fanning' and 'nipping' (Kühme, 1963, 1964b; Fig. 1). Parents are even able to distinguish – using olfactory cues – between their own brood and conspecific, but unrelated, broods. As the young grow, and become more independent, the parents become progressively less responsive to their odour until about 20 days post-hatch, when young would leave their parents for an independent life. In a major study of both African and Central American cichlids (convict cichlid, Jack Dempsey, jewelfish and banded jewelfish), Myrberg (1964) also found that parents are unable to differentiate their own eggs from hetero-specific clutches but, once hatched, parents could use chemical cues to recognise their own species' young. As the fry develop from wrigglers to free-swimming larvae, there is a growing reliance on visual cues, but olfaction is still important. Convict cichlid mothers clearly recognise water that has bathed their own young, even in the absence of visual cues, being able to discriminate their scent from that of other species' fry (Myrberg, 1975); the same is known for Midas cichlid mothers (McKaye and Barlow, 1976). Thus, chemosensory recognition of young is dependent on developmental stage; as wigglers become free-swimming, reliance on visual cues becomes stronger (Myrberg, 1964, 1966). Vision may be more important in 'orienting' to young, whereas 'discrimination' (between their own brood and other conspecific broods, or between conspecific and hetero-specific broods) may require chemical cues. Furthermore, previous brooding experience may 'imprint' the young's scent on the parents (or the parents may 'learn' the scent of their young; Greenberg, 1963; Myrberg, 1964). Exposure to scent from hetero-specific fry causes maternal convict cichlids to become highly agitated, even to the extent of abandoning their own fry, suggestive of detecting 'something dangerous in the water'. However, when given only visual cues, neither parent is able to discriminate conspecific from hetero-specific fry. Conversely, the mother would prefer her own brood, when given only visual access, if she has previously been exposed to chemical cues released by this brood. Parental Midas cichlids retrieve displaced fry and return them to their brood (McKaye and Barlow, 1976). That this occurs at night or in turbid water suggests that chemical cues are important.

Midas cichlid fry prefer (are attracted to) water conditioned by their mother, or another adult female – but not their father – over plain water (Barnett, 1977). However, they prefer water scented by either of their parents' urine over blank water. Yet this response is not specific for their parents' urine; urine of a conspecific adult (either sex) has the same effect. No preference was shown for water scented with their parents' mucus (Barnett, 1981). This is important, because fry eat mucus from their parent's bodies, apparently more so from their father's than from their mother's (Noakes and Barlow, 1973); the response is therefore due to behav-

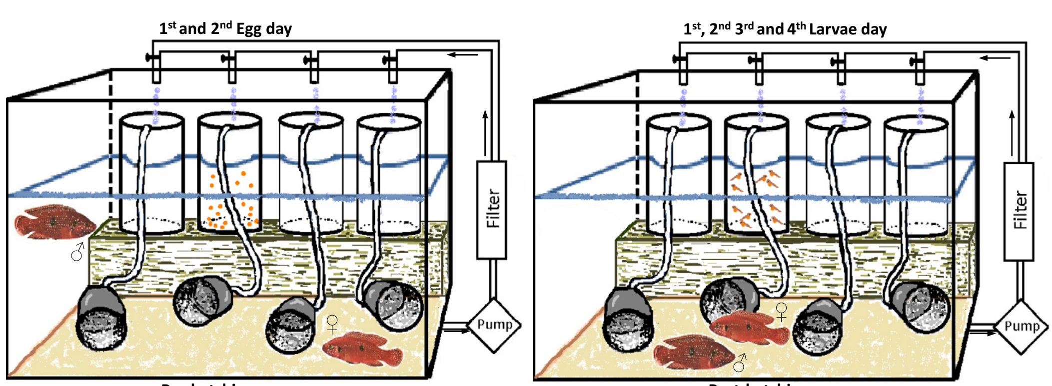

Fig. 1. Redrawing of Kühme's brood care experiments from 1963. For his preference tests, Wolfdietrich Kühme used the West-African Jewel fish (*Hemichromus bimaculatus*), a monogamous substrate-spawner with biparental care, to investigate the importance of chemical signals during brooding (Kühme, 1963). Kühme's test aquarium was equipped with 4 flowerpots serving as potential nesting sites; to each pot belonged a 5 l opaque glass whose margins surpassed the water surface of the aquarium The glass was supplied with water by a leaking tap and a silicon tube constantly delivered the overrun water to the flowerpot's bottom hole. Kühme found that egg care was vision-only-oriented: parents would position themselves in front of dummy eggs or their own eggs presented in a transparent inodorous glass container. But, neither males nor females showed any preference for the flowerpot (here, the second from left) delivering the holding water of their own eggs (left-side drawing). This, however, changed drastically after their larvae started hatching a few days later (right-side drawing). Then, both parents positioned themselves protectively in front of the odorous flowerpot delivering their larvae's scent, whereby females showed the strongest orientation. During their highest brooding motivation, the first 4–5 larval days, females spent much time inside the pot and expressed intense fanning and nipping behaviour.