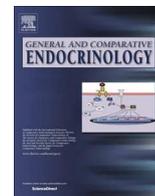




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Chemical communication in cichlids: A mini-review

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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.

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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 (Etioplineae) and Madagascar (Ptychochrominae) cichlids and the more derived Neotropical (Cichlinae) and African (Pseudocrenilabrinae) cichlids (Sparks and Smith, 2004; Streefman et al., 1998). African cichlids (80% of all cichlids) attract

Abbreviations: 17,20 β -P, 17 α ,20 β -dihydroxy-4-pregnen-3-one; 17,20 α -P, 17 α ,20 α -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.

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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 endemism (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 jewel fish (*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, jewel fish and banded jewel fish), 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 wrigglers 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-

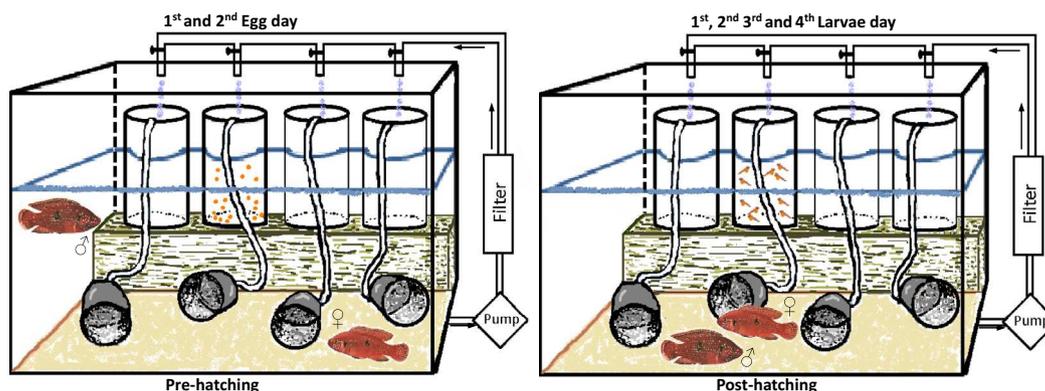


Fig. 1. Redrawing of Kühme's brood care experiments from 1963. For his preference tests, Wolf Dietrich Kühme used the West-African Jewel fish (*Hemichromis bimaculatus*), a monogamous substrate-spawner with biparental care, to investigate the importance of chemical signals during brooding (Kühme, 1963). 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.

our other than simple food-search (Barnett, 1981). Together, these studies suggest that fry can distinguish between the sex of adults using non-urinary odorants and, given a choice, prefer their mother (or at least an adult female). It is the mother that spends more time caring for the brood, whereas the father spends more time defending their territory; attraction to the nearest female is likely to return the fry to its brood, whereas to the father may take it to the edge of their territory. Young convict cichlids prefer the water of their home tank over that of another family (Wisenden and Dye, 2009), suggesting that they can distinguish kin from non-kin on the basis of olfactory cues. However, this preference is labile and can be 'reset' in less than 20 min; young prefer the water they were in, when in visual contact with their parents, rather than the water conditioned by their parents. If they cannot see their parents, however, they still choose home-tank water (Wisenden and Dye, 2009). This is intriguing because it not only suggests a level of olfactory learning (at a young age), rather than imprinting, but also that the odorants involved do not necessarily come from the parents. When young convict cichlids are tested specifically for orientation toward the odour of their parents without the odour of tank mates (including their own odour), they show a preference for the odour of their biological mother over blank water. They also show a preference for the odour of a maternal female with young the same age the young being tested (hormonally-matched maternal female) over blank water, but have no overall preference when presented with the odour of their biological mother versus the odour of a hormonally-matched maternal female (Wisenden et al., 2014). Interestingly, small young prefer the odour of their biological mother over a genetically-unrelated mother but larger young do not. This switch coincides with the timing of a shift in conspecific brood adoption that occurs in this species. Parents preferentially adopt conspecific young that are smaller and weaker swimmers than their own young so that when brood predators attack, it is the adopted young that are most often taken (Wisenden and Keenleyside, 1992, 1994; Wisenden et al., 2015). Although all displaced larval convict cichlids are strongly selected to find the protection of a family on the basis of chemosensory (and visual) cues, those smaller than 7 mm have additional selection to prefer their biological family where they face less exposure to brood predators. Free-swimming jewelfish larvae respond to water conditioned by their siblings by tighter shoaling (Kühme, 1964a); although apparently innate, the response is reduced as the larvae grow. Depending on species and odorant source, then, such olfactory-driven shoaling behaviour in young cichlids may be both innate and/or involve learning.

In an African, maternal mouth-brooding cichlid, the Mozambique tilapia, chemical signals released by the mother (or another reproductively active female, but not non-reproductive female or male) evoke a preference of fry for a 'broody' over a 'non-broody' female model (Russock, 1990). This effect is persistent, and occurs even when the chemical signals are not present, suggesting a learned effect (or at least priming during the first 24 h post fertilization). However, the relative importance of visual and chemical cues is unclear; particularly, whether chemical cues alone could evoke an effect.

The adaptive significance of parent-fry recognition is most likely predation avoidance; in the presence of a threat, fry would gain protection from their parents or – failing that – an adult conspecific, preferably female. Parents able to distinguish their own fry from non-related, conspecific fry would ensure survival of a greater proportion of their own progeny; fry attracted to nearby adult conspecifics, most likely their mother, would be less likely to be eaten. Reliance on chemical cues would be greater at night (to avoid nocturnal predators) or in turbid water. However, the compounds involved have yet to be identified. Clearly urine is a likely route of release, at least in adults, but other routes may be

important. Furthermore, it is as yet unclear whether parental recognition by young is innate, or a result of 'adult imprinting'. These are questions for future research.

3. Reproduction

Chemical communication during reproduction was first investigated in cichlids by (Crapon de Caprona, 1974, 1980); male *Astatotilapia burtoni* (previously *Haplochromis burtoni*) begin courting behaviours, such as 'leading' and display of their dark eye-bar, when exposed to water conditioned by a gravid female. This is not seen in anosmic fish (noses blocked with cotton wool), suggesting the primacy of olfaction. Water conditioned by non-reproductive females does not evoke such strong behavioural responses in males, suggesting that gravid females are releasing more and/or different odorants than non-gravid ones. Furthermore, responses are little affected by the presence or absence of a 'dummy' female, suggesting that olfactory stimuli are more important than visual stimuli. Indeed, males courted blinded *Tilapia mariae* (spotted tilapia) in the same tank in the presence of female-conditioned water; these fish look markedly different from female *A. burtoni*, leading the author to suggest "...once in a reproductive mood, a male *H. burtoni* will court any fish coming in its vicinity!". This is consistent with our observations of male Mozambique tilapia courting goldfish, conspecific males (Oliveira and Almada, 1998), or their own mirror image (Keller-Costa, 2014). Interestingly, these effects on behaviour out-last the exposure to the stimulus, suggesting an effect on the endocrine system.

Male Mozambique tilapia drastically increase their urination frequency in the presence of a female that is near ovulation, but not as much with post-spawn females (Almeida et al., 2005; Miranda et al., 2005). Anosmic males continue to court ripe females but – crucially – fail to increase their urination rate. The cues that evoke the males' increase in urination are olfactory and are contained in the females' urine; however, other routes of release, such as the faeces, cannot be excluded. Electro-olfactogram recordings show that male tilapia are capable of discriminating between pre- and post-spawn females through the smell of their urine (Almeida et al., 2005; Miranda et al., 2005). The nature of the chemical signal of pre-spawn females is as yet unknown, but 17 β -estradiol 3-glucuronate (E2-3-G) is a good candidate; it is a potent olfactory stimulus in tilapia (Hubbard et al., 2014) and detected via a specific olfactory receptor, distinct from that of the male pheromone (Keller-Costa et al., 2014a). Furthermore, pre-ovulatory females release overall more 17 β -estradiol into the water than post-spawn females (Huertas et al., 2014). Since 17 β -estradiol is produced by the growing follicle, it could act as a social cue released by female tilapia, providing information on their reproductive condition.

The urine of male Mozambique tilapia contains (a) pheromone(s) that stimulate(s) the females' reproductive system (Huertas et al., 2014) and lure(s) them to their nest to spawn (Barata et al., unpublished data). 5 β -pregnane-3 α ,17 α ,20 β -triol 3-glucuronate (20 β -P-3-G) and its 20 α -epimer (20 β -P-3-G) constitute the sex pheromone in male tilapia urine that increases the female release of 17,20 β -dihydroxy-pregn-4-en-3-one (17,20 β -P) (Keller-Costa et al., 2014b), the major oocyte maturation-inducing hormone in teleosts. Thus, dominant male tilapia stimulate oocyte maturation in females, thereby priming their mates for ovulation. This likely promotes spawning synchronization – crucial for external fertilizers – to ensure their eggs and sperm are released together (Fig. 2). Whether these two identified steroids also have a releaser effect, influencing female mate-choice and attraction, remains to be tested.

Dominant male Nile tilapia (*Oreochromis niloticus*) release the same pregnanetriol 3 α -glucuronates via their urine and have similar olfactory sensitivity to these steroids as the Mozambique tilapia.

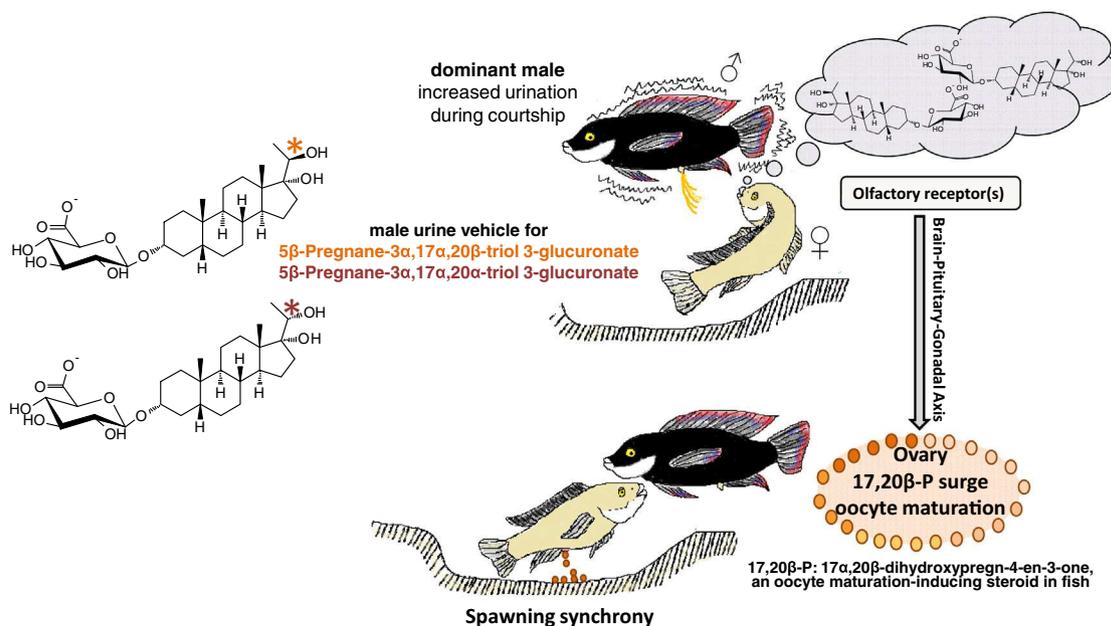


Fig. 2. The sex pheromone of male tilapia primes ovulation. In the lek-breeding Mozambique tilapia (*Oreochromis mossambicus*), reproduction is mediated through urinary cues released by dominant males. Two steroid glucuronates (5β-pregnane-3α,17α,20β-triol 3-glucuronate and its 20α-epimer) are produced in large quantities by dominants and are the most potent urinary odorants to females. They act via (a) specific and common olfactory receptor(s) on the females' endocrine axis, stimulating production and release of 17,20β-P, the major oocyte maturation-inducing hormone in teleost fishes. This leads to the ripening of the oocytes and (likely) synchronizes spawning (Keller-Costa et al., 2014b).

pia (Hubbard et al., 2014). Interestingly, the two closely related species are allopatric which may explain their possible retention of the same chemical signalling system. Burton's mouthbrooder (*A. burtoni*), too, responds to 3α-glucuronidated steroids, i.e. etiocholanolone 3α-glucuronate, 5β-pregnan-3α,17-diol-20one 3α-glucuronate, 5β-pregnan-3α,17α,21-triol-11,20-dione 3α-glucuronate, (Cole and Stacey, 2006). This more derived East African cichlid is able to also detect 17-glucuronidated, 3-sulphated, 17-sulphated, and 3,17-disulphated steroids via distinct olfactory receptors (Cole and Stacey, 2006), an ability that the Mozambique and Nile tilapia apparently lack (Hubbard et al., 2014; Keller-Costa et al., 2014a). However, whether *A. burtoni* releases any of these steroids, and – if so – what their pheromonal functions are, remains to be tested. Nevertheless, that male *A. burtoni*, too, urinate more frequently when exposed to pre-spawn females as compared to mouth-brooding females (Maruska and Fernald, 2012) suggests that a signalling system similar to the Mozambique tilapia exists. As a result of olfactory screening, involving over fifty cichlid species, it has been suggested that the putative pheromone system of *A. burtoni* arose in the African group after their split from the Neotropical cichlids (Stacey, 2010; Stacey and Sorensen, 2009). These results point towards a gradual accumulation of olfactory receptor (OR) types from basal (*Hemichromis*) to derived species such as *A. burtoni* – “EOG responses to our test steroids are seen only in Africans (over 30 species tested), and in all Africans tested except *Heterochromis multidens*, the basal African species” (Stacey and Sorensen, 2009; Fig. 3). Moreover, as in the Mozambique and Nile tilapia and *A. burtoni*, all the cichlids tested are unable to detect unconjugated steroids (Stacey, 2010; Stacey and Sorensen, 2009). In this, (African) cichlids differ from their perciform relatives, the gobies, which apparently also use hormonal steroids as reproductive pheromones. However, although conjugates are probably among the most active and attractive forms released (Colombo et al., 1980; Katare et al., 2011; Tierney et al., 2013), the gobies' olfactory system also responds to unconjugated steroids (Murphy et al., 2001).

In vitro incubation experiments with steroid precursors have shown that conjugation occurs in the testes (Arbuckle et al., 2005; Colombo et al., 1980; Kime and Hyder, 1983; van den Hurk and Resink, 1992) or in accessory testicular glands, also called seminal vesicles (Jasra et al., 2007; Resink et al., 1987; Van den Hurk et al., 1987). Incubation of testes from sexually mature Mozambique tilapia with labeled testosterone yielded large amounts of labelled testosterone- and androstan-glucuronates (Kime and Hyder, 1983). 17,20β-dihydroxypregn-4-en-3-one (17,20β-P) is the major progesterone in fish mainly produced under the control of luteinising hormone (LH) and not only acts as a maturation inducer in females but, in males, to initiate spermatogenesis, enhance sperm motility and promote milt production (reviewed in Scott et al., 2010). Several fishes also produce the epimeric form 17,20α-P, although its exact physiological role is as yet unclear (Scott et al., 2010). 17,20β-P and 17,20α-P and their conjugates are present at higher concentrations in the urine of dominant male Mozambique tilapia than subordinates (Oliveira et al., 1996) and males becoming subordinates show a significant drop in their 17,20β-P and 17,20α-P levels. Studies with several African cichlids have shown that long-term subordinate males have smaller testes, fewer Leydig cells and lower sperm motility, although spermatogenesis continues (Kustan et al., 2012; Maruska and Fernald, 2011; Oliveira and Almada, 1999; Pfennig et al., 2012). Thus, the high levels of 17,20β-P and 17,20α-P measurable in dominant male urine are likely a direct reflection of the males' sperm quality and reproductive ability. However, tilapia cannot smell unconjugated and conjugated 17,20β-P or 17,20α-P (Frade et al., 2002). Nevertheless, metabolism of 17,20α-P and 17,20β-P into pregnanetriols and subsequent 3α-glucuronidation produces water-soluble signals which, expelled in the urine, may be detected by females. The increased availability of 17,20β-P and 17,20α-P in dominant males during spermatogenesis may, indeed, provide the substrate for the increased pheromone concentration in dominant male urine. Thus, it seems that the pregnanetriol 3-glucuronates are an 'honest' and reliable signal, informing the female about the males' reproductive potential.

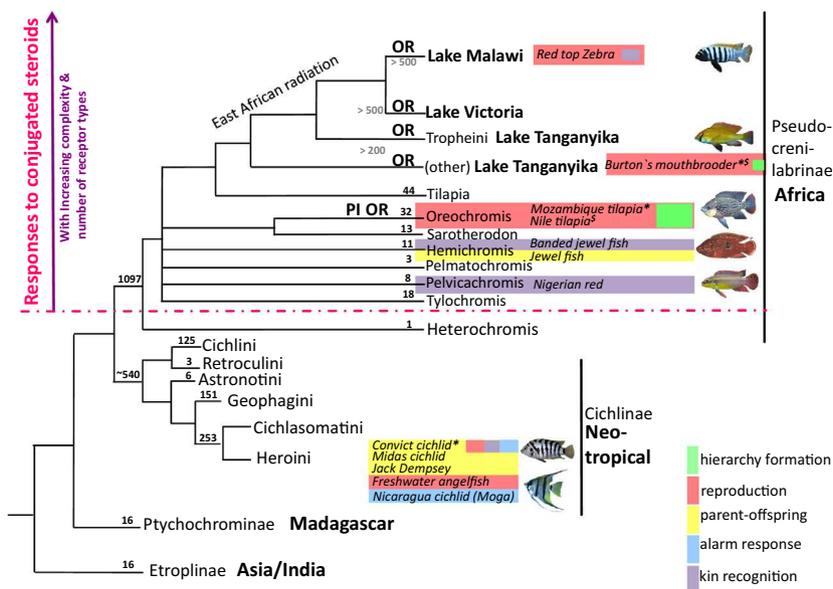


Fig. 3. Simplified schematic cladogram of cichlid intrafamilial relationships (according to Genner et al., 2007; Kocher, 2004; Smith et al., 2008; Stiassny, 1991). Of 1670 described species (Fishbase, 2014b), in only about a dozen cichlids has the role of chemical communication been investigated (coloured bars: green – hierarchy formation; red – reproduction; yellow – parent-offspring recognition; blue – alarm responses; purple – (other) kin recognition). The so far best understood model species are highlighted by an asterisk. Species with their genomes sequenced (Brawand et al., 2014) are indicated by a dollar sign. Black numbers above branches represent number of described species (Fishbase, 2014b). Grey numbers indicate numbers of estimated species in the East African lakes: Lake Tanganyika more than 200 species, Lake Malawi and Lake Victoria each with more than 500 species (Turner et al., 2001). As this cladogram drawing shows, entire tribes and flocks of cichlids have been so far overlooked completely; to our knowledge, no studies have yet addressed chemical communication in the very basal Indian and Madagascan cichlids and reports from Neotropical cichlids are restricted to a handful of representatives in the Heroini tribe. In one African, the Mozambique tilapia, was the chemical identity and function of a cichlid pheromone unveiled (Keller-Costa et al., 2014b; indicated as PI – pheromone identified). Diversity in the ORA and OlfC (vomeronasal type 1 (V1R) and 2 (V2R) homologues) olfactory receptor gene families suggests a contribution of olfaction, including chemical communication, to the species diversification in the cichlid flocks of the East African Lakes (Nikaido et al., 2014, 2013; OR – olfactory receptor genes identified).

Male nutritional state may also be a good indicator of male health and genetic quality. Female Nile tilapia can discriminate between high-protein-fed and low-protein-fed males by olfaction. They spend more time in the vicinity of holding water from well-fed males than conditioned water from males fed with low-protein diet (Giaquinto et al., 2010).

Assortative mating, i.e. preferred mating of similar genotypes/phenotypes, is a widely suggested key mechanism to explain the rapid sympatric speciation events in African cichlids. Whether adult cichlids – especially those from Africa's Rift Valley Lakes – use chemical cues to selectively mate with conspecifics, thereby driving reproductive isolation, is somewhat controversial (Kidd et al., 2006; Plenderleith et al., 2005). While some studies find that visual cues in the form of male nuptial hues are necessary and sufficient to maintain reproductive barriers of co-occurring sister species (e.g. Selz et al., 2014), others conclude that additional chemical information is required for appropriate mate choice (Blais et al., 2009; Plenderleith et al., 2005). Females of the Lake Malawi cichlid *Maylandia emmilotos* (previously *Pseudotropheus emmilotos*) that can fully interact with males, always prefer conspecifics over closely related (sympatric) heterospecific (*Pseudotropheus fainzilberi*) males. In contrast, females with only visual contact show no significant preference for each male type. But females with visual contact and olfactory cues present, again prefer males of their own species (Blais et al., 2009; Plenderleith et al., 2005). Multimodal signalling seems highly plausible; in nature, usually a concert of visual, chemical and acoustic information would be available to the female to obtain reliable information about the (genetic) quality of any potential mate. Yet the relative contribution of the different signal types likely changes between species and contexts, and

variable environmental conditions may require (to some extent) adaptive responses. Unlike many other cichlids used in behavioural research, the South American angelfish (*Pterophyllum scalare*) shows no obvious sexual dimorphism. In the absence of nuptial colouration, pairs of this species show elaborate reproductive behaviours. Either visual or chemical cues emitted by the males increase spawning rates in the females, yet simultaneous presentation of the two stimuli results in even higher spawning rates as compared to only one stimulus being present (Chien, 1973). This additive effect suggests that the two sensory systems modulate reproduction via independent pathways. From studies in the Mozambique tilapia, it seems that physiological and, in particular, hormonal responses often require chemical signals in addition to (or instead of) visual cues (Keller-Costa et al., 2014b; Oliveira et al., 2005). For example, anosmic male tilapia continue to court gravid females but do not increase their urine release (Miranda et al., 2005). Thus, for the behavioural response, only the visual stimulus of a female is needed. For the full pheromonal response (release of the urinary pheromone), the male must be able to smell the female, and judge her ready to spawn.

Sexual imprinting has been suggested to help maintain reproductive isolation among closely related sympatric cichlid species (Verzijden and ten Cate, 2007). An interspecific cross-fostering experiment in the closely related Lake Victoria species *Pundamilia pundamilia* and *Pundamilia nyererei* provides evidence that females prefer males of the maternal phenotype as a result of early learning. Females that, as larvae, were cross-fostered by heterospecific mothers later in life prefer heterospecific males over conspecifics; this does not occur in females fostered by their genetic mother. Since both visual and chemical cues could be used at all stages of

Table 1
Summary of chemical communication studies in cichlid species.

| Origin | Latin name | Common name | Mating ^a | Brood care ^a | Chem. Comm. ^b | Bioassay ^c | Original studies |
|-------------------------|---|---------------------------|-----------------------------------|-------------------------------|---|--|---|
| Central America | <i>Amatitlania siquia</i> and <i>A. nigrofasciata</i> | Convict cichlid | Monogamous; cave-spawner | Bi-parental substrate-brooder | Parent → young, mate and kin recognition; alarming | Choice (w/scented water) and alarm response (w/skin extract) tests | Myrberg (1964, 1966, 1975), Wisenden and Dye, (2009), Wisenden et al. (2014, 2015) Anim Behav, Lee-Jenkins and Godin (2013), Nelson et al. (2013), Roh et al. (2004), Reeb (1994) |
| | <i>Amphilophus citrinellus</i> | Midas cichlid | Monogamous; open-spawner | Bi-parental substrate-brooder | Parent → young and young → parent recognition | Choice tests w/holding water & parental urine & mucus | Barnett (1977, 1981), Noakes and Barlow (1973), McKaye and Barlow (1976) |
| | <i>Rocio octofasciata</i> | Jack Dempsey | Monogamous; open-spawner | Bi-parental substrate-brooder | Parent → young recognition | Choice test by reintroducing young | Myrberg (1964) |
| | <i>Hypsophrys nicaraguensis</i> | Nicaragua cichlid or Moga | Monogamous; open-spawner | Bi-parental substrate-brooder | Alarm response | Exposure to conspecific alarm cue → effects on body shape | Abate et al. (2010) |
| South America | <i>Pterophyllum scalare</i> | Freshwater angelfish | Monogamous; open-spawner | Bi-parental substrate-brooder | Reproduction (induced spawning); alarm response | Exposure to ♂ holding water; fright response to skin extract | Chien (1973), Schutz (1956) |
| North to Central Africa | <i>Oreochromis niloticus</i> | Nile tilapia | Polygamous; lekking; open-spawner | Maternal mouth-brooder | Reproduction; hierarchy formation | Effect of water renewal on aggression and hierarchy; ♀ mate choice; EOGs | Gonçalves-de-Freitas et al. (2008), Giaquinto and Volpato (1997), Giaquinto et al. (2010), Hubbard et al. (2014) |
| Southern Africa | <i>Oreochromis mossambicus</i> | Mozam-bique tilapia | Polygamous; lekking; open-spawner | Maternal mouth-brooder | Young → parent and social status recognition; hierarchy formation; reproduction | Choice tests, resident-intruder paradigms; ♀ endocrine responses; EOGs | Russock (1990), Miranda et al. (2005), Keller-Costa et al. (2012, 2014a,b), Huertas et al. (2014), Barata et al. (2007, unpublished data) |
| East Africa | <i>Astatotilapia burtoni</i> | Burton's mouth-brooder | Polygamous; lekking; open-spawner | Maternal mouth-brooder | Reproduction; social status recognition | Effect of ♀ or ♂ holding water on ♂ behaviour; EOGs; urine signalling | Crapon de Caprona (1974, 1980), Cole and Stacey (2006), Maruska and Fernald (2012) |
| | <i>Haplochromis chilotes</i> ^c | – | Polygamous | Maternal mouth-brooder | Analysis of olfactory receptor genes ORA ^d | – | Ota et al. (2012), Nikaido et al. (2013) |
| | <i>Haplochromis sauvagei</i> ^c | – | Polygamous | Maternal mouth-brooder | Analysis of olfactory receptor genes ORA & OlfC ^e | – | Ota et al. (2012) |
| | <i>Maylandia emmiltos</i> | Red top zebra | Polygamous; open-spawner | Maternal mouth-brooder | Kin-recognition | ♀ choice tests | Plenderleith et al. (2005) |
| West Africa | <i>Hemichromis bimaculatus</i> | Jewel fish | Monogamous; open-spawner | Bi-parental substrate-brooder | Parent-young recognition and swarming response | Choice tests; swimming behaviour in response to holding water | Kühme (1963, 1964a,b) |
| | <i>Hemichromis fasciatus</i> | Banded jewel fish | Monogamous; open-spawner | Bi-parental substrate-brooder | Swarming response | Swimming activities in response to holding water | Kühme (1963, 1964b) |
| | <i>Pelvicachromis taeniatus</i> | Nigerian red | Monogamous; cave-spawner | Bi-parental substrate-brooder | 'Self-odour-recognition' | Choice tests w/scented water | Thünken et al. (2009) |

^a Information (mostly) retrieved from Fishbase 2014.

^b Context(s) where chemical communication mechanisms have been reported to play a role;

^c Bioassay(s) used to investigate chemical communication.

^d ORA olfactory receptor gene family – teleost homologue of the mammalian vomeronasal type 1 receptors (V1R family).

^e OlfC olfactory receptor gene family – teleost homologues of the mammalian vomeronasal type 2 receptors (V2R family).

the experiment, it is possible that imprinting was indeed based on olfactory cues.

Small major histocompatibility complex (MHC) peptides present in body fluids including urine are potent odours for some fishes and have been shown to influence mate choice decision and olfactory imprinting on kin in sticklebacks (Milinski et al., 2005, 2010) and zebrafish (Hinz et al., 2013). MHC molecules are cell-surface glycoproteins involved in adaptive immune responses of vertebrates, and the MHC genotype has been shown to be an important factor determining an individuals' resistance to parasites (Blais et al., 2007). Divergent selection of MHC genes is suggested as driver in reproductive isolation in closely related sympatric African cichlids and could result in species-specific MHC signals that allow odour-mediated assortative mating (Blais et al., 2007).

4. Dominance hierarchies

In hierarchy-forming African cichlids, chemical signals are important to advertise social rank and maintain group stability. Crapon de Caprona (1980) first noted, during investigations into involvement of chemical communication in reproduction of *Astatotilapia burtoni*, that exposure of males to male-conditioned water in contrast to female-conditioned water – evokes increases in attacking and displays of the black eye-bar, a signal of male territoriality or dominance. Evidence of dominant fish using chemical cues to signal their rank exists for at least three different species, the Oreochromine Mozambique (Barata et al., 2007) and Nile (Gonçalves-de-Freitas et al., 2008) tilapias, and the Haplochromine *A. burtoni* (Maruska and Fernald, 2012). Continuously renewed water flow increases attack frequency by subordinate Nile tilapia in agonistic interactions, which can negatively influence the hierarchical stability of a social group (Gonçalves-de-Freitas et al., 2008). Size-matched juvenile Nile tilapia of α and β ranks paired in neighbouring compartments on neutral territory are less aggressive when water exchange is allowed between compartments than in the absence of exchange (Giaquinto and Volpato, 1997). This is observed in familiar (from the same social group) and unfamiliar (from different social groups) fish. However, in the first scenario, reduction in aggressiveness is about twice that observed in fish coming from different groups (Giaquinto and Volpato, 1997). This shows that conspecific chemical cues decrease aggression in Nile tilapia, likely through: (1) a general social status signal, and (2) individual recognition cues. Chemically mediated reduction of aggression is well known also from the closely related Mozambique tilapia; males not only increase their urination frequency in the presence of pre-spawn females, but also during aggressive disputes with rival males (Barata et al., 2008, 2007). The olfactory potency of male urine increases with ascending social rank of the donor which strongly suggests the presence of a dominance pheromone. Although urine production rate is not different, dominant males store much more urine in their bladder, for release during social interactions, than subordinates (Barata et al., 2007). The larger urine storage capacities are facilitated by a more muscular urinary bladder, larger muscle fibres and thicker urothelium (Keller-Costa et al., 2012). Males prevented from urinating (by tying of the genital papilla) engage in significantly more fighting and escalate faster to highly aggression than controls (Keller-Costa et al., 2012). The male displaying the first aggressive behaviour usually goes on to win the fight; this is not the case in tied males. This suggests that a male is able to predict the fighting outcome based on the chemical signals perceived in his rival's urine. Male tilapia responding to their mirror-image, whilst stimulated with dominant male urine, have a slower increase in aggressiveness as compared to males without any chemical stimulus. Stimulation with subordinate male urine has the reverse effect, amplifying highly aggressive behaviours (Barata et al., unpublished data). Together,

these studies demonstrate that urinary dominance signals in male tilapia reduce aggression and increase social stability. The chemical nature of the aggression-reducing urine signal is, however, unresolved. An attempt to tackle the chemical identity suggests that the signal consists of multiple, likely also hydrophilic, substances and is (at least in part) different from the urinary pregnanetriol 3-glucuronates that prime reproduction in females (Keller-Costa, 2014).

Social rank signalling through the urine is also present in the East African *A. burtoni*. Urination frequencies, together with territorial behaviours, of dominant *A. burtoni* males are higher when exposed to a rival male in both visual only and full interaction trials (Maruska and Fernald, 2012). In hierarchy-forming cichlids, reproduction is tightly controlled by social status as changes in social rank quickly, and profoundly, affect all levels of the hypothalamus–pituitary–gonadal axis (Fernald and Maruska, 2012; Maruska and Fernald, 2011; Maruska et al., 2011). Overt behaviours and colouration change within minutes when subordinates obtain the opportunity to ascend in rank. Gonadotropin-releasing hormone I (GnRH1) expression is up-regulated, GnRH brain levels increase already 30 min post-ascend and GnRH1 neurons start to enlarge in volume (Maruska et al., 2011). The GnRH peptides bind to GnRH receptors in the pituitary and induce luteinising hormone (LH) and follicle-stimulating hormone (FSH) synthesis. Released into the blood stream and transported to the testes the gonadotropins stimulate steroid production and spermatogenesis. Rapid changes also occur in the testes; FSH receptor expression increases after 30 min to stimulate steroid production and spermatogenesis. It takes about five days for morphological and structural changes in testicular cell composition to occur (Maruska and Fernald, 2011). In several cichlids, levels of circulating and urinary androgens are higher following social interactions (Hirschenhauser et al., 2008; Oliveira et al., 1996). In *A. burtoni*, Nile and Mozambique tilapia, plasma 11-ketotestosterone (11KT) levels rise quickly as males are acquiring a dominant position (Maruska and Fernald, 2011; Oliveira et al., 1996; Pfennig et al., 2012). Interestingly, visual cues from a larger dominant *A. burtoni* male are sufficient to suppress dominant behaviours and nuptial hue in smaller conspecifics; however, additional sensory cues (i.e. chemical or acoustic) are necessary to alter gene expression, circulating androgens and testis size (Chen and Fernald, 2011).

Understanding how social olfactory information is processed in the teleost brain is challenging and much is still unclear. The neuropeptide arginine-vasotocin (AVT), the teleost homologue of mammalian arginine-vasopressin (AVP), was suggested recently as a putative factor involved in olfactory coding in tilapia (Almeida et al., 2012). AVT has several functions, affecting osmoregulation, cardiovascular- and stress response and also a central effect on social behaviour. In rodents, AVP in the olfactory bulbs modulates olfactory-based social recognition and short-term social odour memory (McEwen, 2004). Male Mozambique tilapia have measurable AVT levels in several brain areas, but the highest levels are found in the pituitary and the olfactory bulb (Almeida et al., 2012). The high AVT levels found in the latter suggest a role for AVT in the processing of olfactory stimuli involved in intra-specific communication in cichlids.

5. Chemical cues and predation risk

A wealth of literature exists describing the behavioural responses to chemical alarm cues in fishes (reviewed by; Ferrari et al., 2010; Wisenden, 2014). Broadly speaking, conspecific-released chemical alarm cues can be divided into 'disturbance cues', released by fish threatened by predation (or other stressor), and 'damage-released alarm cues', which require mechanical damage to the donor (biting by a predator, for example) for their release.

There is evidence for both in cichlids. However, following the original observations of von Frisch (1938), the majority of evidence for damage-released alarm cues comes from ostariophysan fish, chiefly the fathead minnow (*Pimephales promelas*), which were believed to release alarm cue from specialised ‘club cells’ in the skin (this theory is now largely discredited); cichlids do not have such club cells, so cichlid damage-released alarm cues may well be different from other fish (but see Barreto et al., 2010). Indeed, early studies suggested that the alarm response was lacking in cichlids (Schutz, 1956). On the other hand, subsequent studies on alarm cues in cichlids have focused on one species; the convict cichlid. Clearly, to resolve these issues, the chemicals involved need to be identified and their routes and mechanisms of release established, and how widespread this phenomenon is in cichlids.

5.1. Disturbance cues

In one of the first investigations of disturbance cues in cichlids (Jordão, 2004), visual (but not chemical) exposure to a predator caused decreased foraging and increased shelter use in the convict cichlid. Conspecifics, not in visual contact with the predator, but exposed to water conditioned by their threatened brethren increase their spatial occupation, suggesting that chemical disturbance cues may increase both vigilance and exploratory behaviour in the absence of any direct (i.e. visual) evidence for predation threat. However, most fish respond to disturbance cues with reduced movement, and decreased area use; this may be an effect of concentration, as seen with the alarm cue (see below).

In contrast to some crustaceans and tadpoles, convict cichlids do not respond to ammonium as a disturbance cue, nor do they apparently increase NH_4^+ release to the water after exposure to a model predator (Vavrek et al., 2008). However, even if freshwater fish release only 10–20% of nitrogenous waste as urea (rather than ammonium), the effect of increasing water urea concentrations evokes the same anti-predator response as the disturbance cue in convict cichlids (and rainbow trout) – a reduction of movement and foraging (Brown et al., 2012). Consistent with a ‘generalized metabolic byproduct’ (rather than a species-specific cue) as the active component, trout disturbance cue has the same effect on convict cichlids (and *vice versa*). Unfortunately, the authors did not measure urea release rates to check whether this is modified by exposure to predators.

5.2. Damage-released alarm cues

Damage-released alarm cues obviously signify a clear and present danger to conspecifics, much more so than disturbance cues, and the anti-predator behavioural responses would be expected to be consequently more intense. In the convict cichlid, chemical cues released from injured skin induce conspecifics to use shelter more, stay closer to the bottom, reduce aggression and – sometimes – evoke the ‘freezing’ response; all ‘classic’ anti-predator behaviours (Wisenden and Sargent, 1997). However, the effects of a similar stimulus derived from mosquito fish (*Gambusia affinis*) are qualitatively and quantitatively different, suggesting a degree of species-specificity in the cichlid alarm cue. This study used injury-released stimulus (i.e. cut skin), always freshly prepared, *not* frozen homogenized skin-extract; alarm cues, almost by definition, are rapidly degraded (Chivers et al., 2013). Similar behavioural responses are seen in free-swimming convict cichlid larvae under parental care: increased shoaling and avoidance of the area containing the alarm cue (Alemadi and Wisenden, 2002). The quality of the donor affects the behavioural response (anti-predator; movement, schooling and area use) to alarm cues in receivers quantitatively (Brown et al., 2004; Roh et al., 2004). However, whether this is due to quantity or quality of the signal is not clear.

Furthermore, the concentration of alarm cue may determine the behavioural responses; low concentrations evoke a subtle switch of feeding behaviour from energy-efficient, head-down foraging to the less efficient – but more vigilant – head-up foraging (Foam et al., 2005). Foraging rates and aggression remain at control levels; only the manner changes, suggesting that low levels of alarm cue alert conspecifics to higher state of vigilance, rather than inducing potentially more costly anti-predator behaviours (much like disturbance cues; see above). In a similar vein, the context in which the alarm cue is perceived may modify the behavioural response; single convict cichlids respond in an ‘all-or-nothing’ manner, and at low concentrations, whereas large groups (6) respond in a graded, concentration-dependent way (Brown et al., 2006). Clearly, ‘safety in numbers’ applies to the perceived threat of alarm cues. Intriguingly, convict cichlids may ‘learn’ to associate predator odour with danger during the embryonic phase if exposed to this odour together with alarm cue (Nelson et al., 2013). This is the first demonstration of such associative learning during embryonic development in a fish, and clearly raises many questions for future research.

Although the chemical nature of the alarm cue in cichlids is unknown, all the above studies used skin as its source. Obviously, more violent predation may result in the prey’s blood being released to the water, as well as damaged skin. Accordingly, Barreto et al. (2013) suggest that blood, too, contains (an) alarm cue; conspecific blood, added to the water, reduced movement and increased latency to feed in the Nile tilapia. Again, some degree of species-specificity was apparent; blood from the unrelated swordtail (*Xiphophorus helleri*) did not have the same effect. Whether the blood-borne alarm cue is the same as the damage-released alarm cue is unclear; time – and analytic chemistry – may tell.

Alarm cues may affect not just behaviour, but also growth and reproductive strategies. In the convict cichlid, short-term exposure to conspecific skin extract (damage-released alarm cue) decreases movement and foraging (classic anti-predator behaviour), as expected (Pollock et al., 2005). However, long-term exposure to the same stimulus also caused slower growth, most likely due to the inhibition of foraging, and earlier reproduction. High predation pressure often induces prey species to reproduce earlier, favouring investment in reproduction over somatic growth due to the increased chance of being eaten as you get older (for example, see Reznick et al., 1996). High predation pressure may also modify body morphology in fish, wherein a deeper-bodied fish would require a predator with a larger gape, and so reduce predation risk (Brönmark and Miner, 1992). Long-term exposure to alarm cues may be the underlying cause (Stabell and Lwin, 1997). Alarm cues may also modulate body morphology in cichlids; exposure to conspecific alarm cue caused a change in body shape (relative body depth) in the ‘moga’ (*Hypsophrys nicaraguensis*), but only at the vulnerable early juvenile stage (Abate et al., 2010). This effect shows some degree of species-specificity in that the zebrafish alarm cue has no such effect.

6. Individual recognition

Although not much is known, it is possible that cichlids can distinguish individuals on the basis of smell. For example, the African cichlid *Pelvicachromis taeniatus* differentiates between its own odour, and those of familiar and unfamiliar conspecifics, suggesting the learning of ‘signatures’ (Thünken et al., 2009). Such ‘signature mixtures’ are defined as “variable subsets of molecules of an animal’s chemical profile” and their release is not necessarily also beneficial to the sender (Wyatt, 2010). Hence, there is no uniform signature mixture; in contrast, it is the differences in the animals’ profiles that allow differentiation (Wyatt, 2010). Individual recog-

nition through chemical cues is suggested by female convict cichlids which can distinguish between their mate and an unfamiliar male conspecific in the dark (Reebs, 1994); nest-guarding females always attack unfamiliar males, whereas their mate is left unmolested. However, the contribution of olfaction or taste, and the route of release of such chemical cues, again, remain unclear.

7. Chemosensory receptors in cichlids

Odorants – including those mediating chemical communication – are detected by their binding to chemosensory G protein-coupled receptors (GPCRs) in sensory neurones of the olfactory epithelium (fish lack a vomeronasal organ or accessory olfactory system). Broadly speaking, fish chemosensory receptors in the olfactory system belong to the same GPCR gene families as tetrapods (but with key differences); these are the ‘olfactory receptors’ (ORs), ‘vomeronasal type 1 receptors’ (V1R or ORA), ‘vomeronasal type 2 receptors’ (V2R or OlfC) and ‘trace amine-associated receptors’ (TAARs). At present, little is known of the function of these families in cichlids. However, the recent sequencing of the genomes of five African cichlids (Nile tilapia, *A. burtoni*, *Maylandia zebra*, *Neolamplogus pulcher*, *Pundamilia nyererei* (Brawand et al., 2014) has allowed examination and comparison of the olfactory receptor genes in these species (Azzouzi et al., 2014). The V1R (ORA) gene family is highly conserved in cichlids (as in other teleosts), consisting of only six genes (Nikaido et al., 2014; Ota et al., 2012). In contrast, the other olfactory receptor gene families (OR, V2R/OlfC and TAAR) have large and variable gene repertoires with a remarkable expansion of the OR and V2R (OlfC) genes, respectively, specific to the cichlid lineage (Azzouzi et al., 2014; Nikaido et al., 2013). This follows suggestions that the conservation or expansion of certain olfactory gene families could play an integral role in the massive speciation of the Rift Valley cichlids (Nikaido et al., 2014, 2013). The authors of these studies hypothesize that the V2R (OlfC) repertoire of cichlids may be involved in detecting amino acids (Nikaido et al., 2013), whereas V1R (ORA) receptors may be involved in pheromone detection (Nikaido et al., 2014). Thus, this field promises much to identify the role(s) of chemical communication in reproductive isolation and speciation through the evolution of pheromone systems. However, this must be accompanied by identification of the pheromones, or other chemical cues, in question and the receptors they act through.

8. Conclusions

From the above, it is clear that cichlids use chemical communication in a variety of contexts. However, it is also clear that much remains to be discovered. One major bottleneck is, we believe, the lack of information on the identities of the chemicals involved (only one cichlid pheromone has been identified to date; compare this, for example, with the number of insect pheromones that have been fully characterized). More knowledge on the types of chemicals involved would allow better directed investigation into the mechanisms and regulation of synthesis and routes of release, and a more precise assessment of the relative importance in interactions using multi-modal signalling. Crucially, too, it would also shed more light on the role of reproductive pheromones in reproductive isolation and speciation in the African Rift cichlids.

The other major bottleneck is, of course, the small number of species that have been investigated in any depth. Most of the work on cichlid alarm cues, for example, has been carried out on one Central American species; do African cichlids use alarm cues in the same way? Little is known about chemical communication in any Indian or Madagascan species. Here, cichlids are – in a sense – victims of their own success. Such a dazzling variety of species,

colours, behaviours and niches probably reflects a similar variety in chemical communication. However, using Krogh’s principal, we believe that this means that there is an ideal cichlid species to address an equal variety of questions in chemical communication. We encourage the scientific community to use an appropriate variety of experimental approaches to the issue.

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References

- Abate, M.E., Eng, A.G., Kaufman, L., 2010. Alarm cue induces an antipredator morphological defense in juvenile Nicaragua cichlids *Hypsophrys nicaraguensis*. *Curr. Zool.* 56, 36–42.
- Alemadi, S.D., Wisenden, B.D., 2002. Antipredator response to injury-released chemical alarm cues by convict cichlid young before and after independence from parental protection. *Behaviour* 139, 603–611.
- Almeida, O., Gozdowska, M., Kulczykowska, E., Oliveira, R.F., 2012. Brain levels of arginine-vasotocin and isotocin in dominant and subordinate males of a cichlid fish. *Horm. Behav.* 61, 212–217.
- Almeida, O.G., Miranda, A., Hubbard, P.C., Frade, P., Barata, E.N., Canário, A.V.M., 2005. Urine as a social signal in the Mozambique tilapia (*Oreochromis mossambicus*). *Chem. Senses* 30, i309–i310.
- Arbuckle, W.J., Belanger, A.J., Corkum, L.D., Zielinski, B.S., Li, W.M., Yun, S.S., Bachynski, S., Scott, A.P., 2005. In vitro biosynthesis of novel 5 β -reduced steroids by the testis of the round goby, *Neogobius melanostomus*. *Gen. Comp. Endocrinol.* 140, 1–13.
- Azzouzi, N., Barloy-Hubler, F., Galibert, F., 2014. Inventory of the cichlid olfactory receptor gene repertoires: identification of olfactory genes with more than one coding exon. *BMC Genomics* 15, 586.
- Baerends, G.P., 1991. Forward. In: Keenleyside, M.H.A. (Ed.), *Cichlid Fishes. Behaviour, Ecology and Evolution*, pp. xiii–xv: Chapman & Hall.
- Baerends, G.P., Baerends van Roon, J.M., 1950. An introduction to the study of the ethology of cichlid fishes. *Behaviour* 1 (Suppl.), 1–243.
- Barata, E.N., Fine, J.M., Hubbard, P.C., Almeida, O.G., Frade, P., Sorensen, P.W., Canário, A.V.M., 2008. A sterol-like odorant in the urine of Mozambique tilapia males likely signals social dominance to females. *J. Chem. Ecol.* 34, 438–449.
- Barata, E.N., Hubbard, P.C., Almeida, O.G., Miranda, A., Canário, A.V.M., 2007. Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*, Peters 1852). *BMC Biol.* 5.
- Barlow, G.W., 2000. *The Cichlid Fishes*. Persus Publishing, Cambridge.
- Barnett, C., 1977. Chemical recognition of mother by young of the cichlid fish, *Cichlasoma citrinellum*. *J. Chem. Ecol.* 3, 461–466.
- Barnett, C., 1981. The role of urine in parent–offspring communication in a cichlid fish. *Zeitschrift Für Tierpsychologie* 55, 173–182.
- Barreto, R.E., Barbosa, A., Giassi, A.C.C., Hoffmann, A., 2010. The ‘club’ cell and behavioural and physiological responses to chemical alarm cues in the Nile tilapia. *Mar. Freshw. Behav. Physiol.* 43, 75–81.
- Barreto, R.E., Miyai, C.A., Sanches, F.H.C., Giaquinto, P.C., Delicio, H.C., Volpato, G.L., 2013. Blood cues induce antipredator behavior in Nile tilapia conspecifics. *PLoS ONE* 8, e54642.
- Blais, J., Plenderleith, M., Rico, C., Taylor, M.I., Seehausen, O., van Oosterhout, C., Turner, G.F., 2009. Assortative mating among Lake Malawi cichlid fish populations is not simply predictable from male nuptial colour. *BMC Evol. Biol.* 9.
- Blais, J., Rico, C., van Oosterhout, C., Cable, J., Turner, G.F., Bernatchez, L., 2007. MHC adaptive divergence between closely related and sympatric African cichlids. *PLoS ONE* 2, e734.
- Brawand, D., Wagner, C.E., Li, Y.L., Malinsky, M., Keller, I., Fan, S., Simakov, O., Ng, A.Y., Lim, Z.W., Bezaul, E., et al., 2014. The genomic substrate for adaptive radiation in African cichlid fish. *Nature* 513, 375–381.
- Brönmark, C., Miner, J.G., 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258, 1348–1350.
- Brown, G.E., Bongiorno, T., DiCapua, D.M., Ivan, L.I., Roh, E., 2006. Effects of group size on the threat-sensitive response to varying concentrations of chemical alarm cues by juvenile convict cichlids. *Can. J. Zool.* 84, 1–8.
- Brown, G.E., Foam, P.E., Cowell, H.E., Guevara-Fiore, P., Chivers, D.P., 2004. Production of chemical alarm cues in convict cichlids: the effects of diet, body condition and ontogeny. *Ann. Zool. Fenn.* 41, 487–499.
- Brown, G.E., Jackson, C.D., Malka, P.H., Jacques, É., Couturier, M.-A., 2012. Disturbance cues in freshwater prey fishes: does urea function as an ‘early warning cue’ in juvenile convict cichlids and rainbow trout? *Curr. Zool.* 58, 250–259.

- Chen, C.C., Fernald, R.D., 2011. Visual information alone changes behavior and physiology during social interactions in a cichlid fish (*Astatotilapia burtoni*). *PLoS ONE* 6.
- Chien, A.K., 1973. Reproductive behaviour of the angelfish *Pterophyllum scalare* (Pisces: Cichlidae) II. Influence of male stimuli upon the spawning rate of females. *Anim. Behav.* 21, 457–463.
- Chivers, D.P., Dixon, D.L., White, J.R., McCormick, M.I., Ferrari, M.C.O., 2013. Degradation of chemical alarm cues and assessment of risk throughout the day. *Ecol. Evol.* 3, 3925–3934.
- Cole, T.B., Stacey, N.E., 2006. Olfactory responses to steroids in an African mouth-brooding cichlid, *Haplochromis burtoni* (Günther). *J. Fish Biol.* 68, 661–680.
- Colombo, L., Marconato, A., Belvedere, P.C., Frisco, C., 1980. Endocrinology of teleost reproduction. A testicular steroid pheromone in the black goby, *Gobius jozo* L. *Bollettino Zoologico* 47, 355–364.
- Crapon de Caprona, M.D., 1974. The effect of chemical stimuli from conspecifics on the behavior of *Haplochromis burtoni* (Cichlidae, Pisces). *Experientia* 30, 1394–1395.
- Crapon de Caprona, M.D., 1980. Olfactory communication in a cichlid fish, *Haplochromis burtoni*. *Zeitschrift für Tierpsychologie* 52, 113–134.
- Fernald, R.D., Maruska, K.P., 2012. Social information changes the brain. *Proc. Natl. Acad. Sci. U.S.A.* 109, 17194–17199.
- Ferrari, M.C.O., Wisenden, B.D., Chivers, D.P., 2010. Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Can. J. Zool.* 88, 698–724.
- Fishbase (2014). Family Cichlidae – Cichlids. www.fishbase.org: Fishbase.
- Fishbase (2014). List of Nominal Species of Cichlidae. In: Froese, R., Pauly, D. (Eds.), www.fishbase.org: FishBase.
- Foam, P.E., Harvey, M.C., Mirza, R.S., Brown, G.E., 2005. Heads up: juvenile convict cichlids switch to threat-sensitive foraging tactics based on chemosensory information. *Anim. Behav.* 70, 601–607.
- Frade, P., Hubbard, P.C., Barata, E.N., Canário, A.V.M., 2002. Olfactory sensitivity of the Mozambique tilapia to conspecific odours. *J. Fish Biol.* 61, 1239–1254.
- Genner, M.J., Seehausen, O., Lunt, D.H., Joyce, D.A., Shaw, P.W., Carvalho, G.R., Turner, G.F., 2007. Age of Cichlids: new dates for ancient lake fish radiations. *Mol. Biol. Evol.* 24, 1269–1282.
- Giaquinto, P.C., Berbert, C.M.D., Delicio, H.C., 2010. Female preferences based on male nutritional chemical traits. *Behav. Ecol. Sociobiol.* 64, 1029–1035.
- Giaquinto, P.C., Volpato, G.L., 1997. Chemical communication, aggression, and conspecific recognition in the fish Nile tilapia. *Physiol. Behav.* 62, 1333–1338.
- Gonçalves-de-Freitas, E., Teresa, F.B., Gomes, F.S., Giaquinto, P.C., 2008. Effect of water renewal on dominance hierarchy of juvenile Nile tilapia. *Appl. Anim. Behav. Sci.* 112, 187–195.
- Greenberg, B., 1963. Parental behaviour and recognition of young in *Cichlasoma biocellatum*. *Anim. Behav.* 11, 578–582.
- Greenwood, P.K., 1991. Speciation. In: Keenleyside, M.H.A. (Ed.), *Cichlid Fishes. Behaviour, Ecology and Evolution*, Chapman & Hall, London, pp. 86–102.
- Hinz, C., Namekawa, R., Behrmann-Godel, J., Oppelt, C., Jaeschke, A., Müller, A., Friedrich, R.W., Gerlach, G., 2013. Olfactory imprinting is triggered by MHC peptide ligands. *Sci. Rep.* 3.
- Hirschenhauser, K., Canario, A.V.M., Ros, A.F.H., Taborsky, M., Oliveira, R.F., 2008. Social context may affect urinary excretion of 11-ketotestosterone in African cichlids. *Behaviour* 145, 1367–1388.
- Hubbard, P.C., Mota, V.C., Keller-Costa, T., da Silva, J.P., Canário, A.V.M., 2014. Chemical communication in tilapia: a comparison of *Oreochromis mossambicus* with *O. niloticus*. *Gen. Comp. Endocrinol.* 207, 13–20.
- Huertás, M., Almeida, O.G., Canário, A.V.M., Hubbard, P.C., 2014. Tilapia male urinary pheromone stimulates female reproductive axis. *Gen. Comp. Endocrinol.* 196, 106–111.
- Jasra, S.K., Arbuckle, W.J., Corkum, L.D., Li, W.M., Scott, A.P., Zielinski, B., 2007. The seminal vesicle synthesizes steroids in the round goby *Neogobius melanostomus*. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 148, 117–123.
- Johnson, T.C., Scholz, C.A., Talbot, M.R., Kelts, K., Ricketts, R.D., Ngobi, G., Beuning, K., Ssemmanda, I., McGill, J.W., 1996. Late pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273, 1091–1093.
- Jordão, L.C., 2004. Disturbance chemical cues determine changes in spatial occupation by the convict cichlid *Archocentrus nigrofasciatus*. *Behav. Process.* 67, 453–459.
- Karlson, P., Lüscher, M., 1959. 'Pheromones': a new term for a class of biologically active substances. *Nature* 183, 55–56.
- Katara, Y.K., Scott, A.P., Laframboise, A.J., Li, W., Alyasha'e, Z., Caputo, C.B., Loeb, S.J., Zielinski, B., 2011. Release of free and conjugated forms of the putative pheromonal steroid 11-oxo-etiocholanolone by reproductively mature male round goby (*Neogobius melanostomus* Pallas, 1814). *Biol. Reprod.* 84, 288–298.
- Keenleyside, M.H.A., 1991. Cichlid fishes – behaviour, ecology and evolution; chapters 8–11. Chapman & Hall, London, UK.
- Keller-Costa, T., 2014. Chemical Identification of Dominance Pheromones in Mozambique Tilapia Males (Ph.D.). Department of Biology, University of Evora, Evora. p. 179.
- Keller-Costa, T., Canario, A.V.M., Hubbard, P.C., 2014a. Olfactory sensitivity to steroid glucuronates in Mozambique tilapia suggests two distinct and specific receptors for pheromone detection. *J. Exp. Biol.* 217, 4203–4212.
- Keller-Costa, T., Hubbard, P.C., Paetz, C., Nakamura, Y., da Silva, J.P., Rato, A., Barata, E.N., Schneider, B., Canário, A.V.M., 2014b. Identity of a tilapia pheromone released by dominant males that primes females for reproduction. *Curr. Biol.* 24, 2130–2135.
- Keller-Costa, T., Lopes, O.S., Almeida, O.G., Hubbard, P.C., Iacovella, A., Lima, M., Barata, E.N., Canário, A.V.M., 2012. Muscular hypertrophy of urinary bladders in dominant tilapia facilitates the control of aggression through urinary signals. *Behaviour* 149, 953–975.
- Kidd, M.R., Danley, P.D., Kocher, T.D., 2006. A direct assay of female choice in cichlids: all the eggs in one basket. *J. Fish Biol.* 68, 373–384.
- Kime, D.E., Hyder, M., 1983. The effect of temperature and gonadotropin on testicular steroidogenesis in *Sarotherodon* (*tilapia*) *mossambicus* in vitro. *Gen. Comp. Endocrinol.* 50, 105–115.
- Kocher, T.D., 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nat. Rev. Genet.* 5, 288–298.
- Kühme, W., 1964a. Eine chemisch ausgelöste Schwarmreaktion bei jungen Cichliden (Pisces). *Naturwissenschaften* 51, 120–121.
- Kühme, W.D., 1963. Chemisch ausgelöste Brutpflege- und Schwarmreaktion bei *Hemicromis bimaculatus* (Pisces). *Zeitschrift für Tierpsychologie* 20, 688–704.
- Kühme, W.D., 1964b. Eine chemisch ausgelöste Brutpflegereaktion bei Cichliden (Pisces). *Die Naturwissenschaften* 51, 20–21.
- Kustan, J.M., Maruska, K.P., Fernald, R.D., 2012. Subordinate male cichlids retain reproductive competence during social suppression. *Proc. R. Soc. B Biol. Sci.* 279, 434–443.
- Lee-Jenkins, S.S.Y., Godin, J.-G.J., 2013. Concurrent effects of familiarity and kinship on social affiliations in convict cichlid (*Amatitlania siquia*) young. *Behaviour* 150, 895–919.
- Maruska, K.P., Fernald, R.D., 2011. Plasticity of the reproductive axis caused by social status change in an African cichlid fish: II. Testicular gene expression and spermatogenesis. *Endocrinology* 152, 291–302.
- Maruska, K.P., Fernald, R.D., 2012. Contextual chemosensory urine signaling in an African cichlid fish. *J. Exp. Biol.* 215, 68–74.
- Maruska, K.P., Levavi-Sivan, B., Biran, J., Fernald, R.D., 2011. Plasticity of the reproductive axis caused by social status change in an African cichlid fish: I. Pituitary gonadotropins. *Endocrinology* 152, 281–290.
- Mayer, W.E., Tichy, H., Klein, J., 1998. Phylogeny of African cichlid fishes as revealed by molecular markers. *Heredity* 80, 702–714.
- McEwen, B., 2004. *The Roles of Vasopressin and Oxytocin in Memory-Processing*. Elsevier Academic Press.
- McKaye, K.R., Barlow, G.W., 1976. Chemical recognition of young by the Midas cichlid, *Cichlasoma citrinellum*. *Copeia*, 276–282.
- Milinski, M., Griffiths, S., Wegner, K.M., Reusch, T.B.H., Haas-Assenbaum, A., Boehm, T., 2005. Mate choice decisions of stickleback females predictably modified by MHC peptide ligands. *Proc. Natl. Acad. Sci. U.S.A.* 102, 4414–4418.
- Milinski, M., Griffiths, S.W., Reusch, T.B.H., Boehm, T., 2010. Costly major histocompatibility complex signals produced only by reproductively active males, but not females, must be validated by a 'maleness signal' in three-spined sticklebacks. *Proc. R. Soc. B Biol. Sci.* 277, 391–398.
- Miranda, A., Almeida, O.G., Hubbard, P.C., Barata, E.N., Canário, A.V.M., 2005. Olfactory discrimination of female reproductive status by male tilapia (*Oreochromis mossambicus*). *J. Exp. Biol.* 208, 2037–2043.
- Murphy, C.A., Stacey, N.E., Corkum, L.D., 2001. Putative steroidal pheromones in the round goby, *Neogobius melanostomus*: olfactory and behavioral responses. *J. Chem. Ecol.* 27, 443–470.
- Myrberg, A.A., 1964. An analysis of the preferential care of eggs and young by adult cichlid fishes. *Zeitschrift für Tierpsychologie* 21, 53–98.
- Myrberg, A.A., 1975. The role of chemical and visual stimuli in the preferential discrimination of young by the cichlid fish *Cichlasoma nigrofasciatum* (Günther). *Zeitschrift für Tierpsychologie* 37, 274–297.
- Myrberg Jr., A.A., 1966. Parental recognition of young in cichlid fishes. *Anim. Behav.* 14, 565–571.
- Nelson, A.B., Alemadi, S.D., Wisenden, B.D., 2013. Learned recognition of novel predator odour by convict cichlid embryos. *Behav. Ecol. Sociobiol.* 67, 1269–1273.
- Nikaido, M., Ota, T., Hirata, T., Suzuki, H., Satta, Y., Aibara, M., Mzighani, S.I., Sturmhuber, C., Hagino-Yamagishi, K., Okada, N., 2014. Multiple episodic evolution events in V1R receptor genes of East-African cichlids. *Genome Biol. Evol.* 6, 1135–1144.
- Nikaido, M., Suzuki, H., Toyoda, A., Fujiyama, A., Hagino-Yamagishi, K., Kocher, T.D., Carleton, K., Okada, N., 2013. Lineage-specific expansion of vomeronasal type 2 receptor-like (V1R) genes in cichlids may contribute to diversification of amino acid detection systems. *Genome Biol. Evol.*
- Noakes, D.L.G., Barlow, G.W., 1973. Ontogeny of parent-contacting in young *Cichlasoma citrinellum* (Pisces, Cichlidae). *Behaviour* 46, 221–255.
- Oliveira, R.F., Almada, V.C., 1998. Mating tactics and male-male courtship in the lek-breeding cichlid *Oreochromis mossambicus*. *J. Fish Biol.* 52, 1115–1129.
- Oliveira, R.F., Almada, V.C., 1999. Male display characters, gonadal maturation and androgens in the cichlid fish *Oreochromis mossambicus*. *Acta Ethol.* 2, 67–70.
- Oliveira, R.F., Almada, V.C., Canario, A.V.M., 1996. Social modulation of sex steroid concentrations in the urine of male cichlid fish *Oreochromis mossambicus*. *Horm. Behav.* 30, 2–12.
- Oliveira, R.F., Carneiro, L.A., Canário, A.V.M., 2005. No hormonal response in tight fights. *Nature* 437, 207–208.
- Ota, T., Nikaido, M., Suzuki, H., Hagino-Yamagishi, K., Okada, N., 2012. Characterization of V1R receptor (ora) genes in Lake Victoria cichlids. *Gene* 499, 273–279.
- Pfennig, F., Kurth, T., Meissner, S., Standke, A., Hoppe, M., Zieschang, F., Reitmayer, C., Goebel, A., Kretschmar, G., Gutzeit, H.O., 2012. The social status of the male

- Nile tilapia (*Oreochromis niloticus*) influences testis structure and gene expression. *Reproduction* 143, 71–84.
- Plenderleith, M., van Oosterhout, C., Robinson, R.L., Turner, G.F., 2005. Female preference for conspecific males based on olfactory cues in a Lake Malawi cichlid fish. *Biol. Lett.* 1, 411–414.
- Pollock, M.S., Zhao, X., Brown, G.E., Kusch, R.C., Pollock, R.J., Chivers, D.P., 2005. The response of convict cichlids to chemical alarm cues: an integrated study of behaviour, growth and reproduction. *Ann. Zool. Fenn.* 42, 485–495.
- Reeb, S.G., 1994. Nocturnal mate recognition and nest guarding by female convict cichlids (Pisces, Cichlidae, *Cichlasoma nigrofasciatum*). *Ethology* 96, 303–312.
- Resink, J.W., van den Hurk, R., van Zoelen, R.F.O.G., Huisman, E.A., 1987. The seminal vesicle as source of sex attracting substances in the African catfish, *Clarias gariepinus*. *Aquaculture* 63, 115–127.
- Reznick, D.N., Butler, M.J., Rodd, F.H., Ross, P., 1996. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* 50, 1651–1660.
- Ribbink, A.J., 1991. Distribution and ecology of the cichlids of the African Great Lakes. In: Keenleyside, M.H.A. (Ed.), *Cichlid Fishes: Behaviour, Ecology and Evolution*. Chapman & Hall, London, pp. 37–38.
- Roh, E., Mirza, R.S., Brown, G.E., 2004. Quality or quantity? The role of donor condition in the production of chemical alarm cues in juvenile convict cichlids. *Behaviour* 141, 1235–1248.
- Russock, H.I., 1990. The effect of natural chemical stimuli on the preferential behaviour of *Oreochromis mossambicus* (Pisces: Cichlidae) fry to maternal models. *Behaviour* 115, 315–326.
- Schutz, F., 1956. Vergleichende Untersuchungen über die Schreckreaktion bei Fischen und deren Verbreitung. *Zeitschrift Für Vergleichende Physiologie* 38, 84–135.
- Scott, A., Sumpter, D.J.T., Stacey, N., 2010. The role of the maturation-inducing steroid 17,20 β -dihydroxypregn-4-en-3-one, in male fishes: a review. *J. Fish Biol.* 76, 183–224.
- Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R., van der Sluijs, I., Schneider, M.V., Maan, M.E., Tachida, H., et al., 2008. Speciation through sensory drive in cichlid fish. *Nature* 455, 620–626.
- Selz, O.M., Pierottia, M.E.R., Maana, M.E., Schmid, C., Seehausen, O., 2014. Female preference for male color is necessary and sufficient for assortative mating in 2 cichlid sister species. *Behav. Ecol.* 25, 612–626.
- Smith, W.L., Chakrabarty, P., Sparks, J.S., 2008. Phylogeny, taxonomy, and evolution of Neotropical cichlids (Teleostei: Cichlidae: Cichlinae). *Cladistics* 24, 625–641.
- Sorensen, P.W., Wisenden, B.D., 2014. *Fish Pheromones and Related Cues*. John Wiley & Sons Inc, Ames.
- Sparks, J.S., Smith, W.L., 2004. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). *Cladistics* 20, 501–517.
- Stabell, O.B., Lwin, M.S., 1997. Predator-induced phenotypic changes in crucian carp are caused by chemical signals from conspecifics. *Environ. Biol. Fishes* 49, 145–149.
- Stacey, N., 2010. Hormonally derived sex pheromones in fishes. In: Norris, D.O., Lopez, K.H. (Eds.), *Hormones and Reproduction of Vertebrates*. Elsevier, San Diego, vol. 1-Fishes, pp. 169–192.
- Stacey, N., Sorensen, P., 2009. Hormonal pheromones in fish. In: Pfaff, D.W., Arnold, A.P., Etgen, A.M., Fahrback, S.E., Rubin, R.T. (Eds.) *Hormones, Brain and Behavior*. Academic Press, San Diego, vol. 1, pp. 639–681.
- Stiassny, M.L.J., 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. In: Keenleyside, M.H.A. (Ed.), *Cichlid Fishes: Behaviour, Ecology and Evolution*. Chapman & Hall, London.
- Streelman, J.T., Zardoya, R., Meyer, A., Karl, S.A., 1998. Multilocus phylogeny of cichlid fishes (Pisces: Perciformes): evolutionary comparison of microsatellite and single-copy nuclear loci. *Mol. Biol. Evol.* 15, 798–808.
- Thünken, T., Waltschky, N., Bakker, T., Kullmann, H., 2009. Olfactory self-recognition in a cichlid fish. *Anim. Cogn.* 12, 717–724.
- Tierney, K.B., Kereliuk, M., Katare, Y.K., Scott, A.P., Loeb, S.J., Zielinski, B., 2013. Invasive male round gobies (*Neogobius melanostomus*) release pheromones in their urine to attract females. *Can. J. Fish. Aquat. Sci.* 70, 393–400.
- Turner, G.F., Seehausen, O., Knight, M.E., Allender, C.J., Robinson, R.L., 2001. How many species of cichlid fishes are there in African lakes? *Mol. Ecol.* 10, 793–806.
- van den Hurk, R., Resink, J.W., 1992. Male reproductive system as sex pheromone producer in teleost fish. *J. Exp. Zool.* 261, 204–213.
- Van den Hurk, R., Resink, J.W., Voorthuis, P.K., 1987. An enzyme-histochemical study concerning the localization of steroid glucuronide production in the reproductive-organs of African catfish, *Clarias gariepinus*. *Aquaculture* 63, 89–96.
- Vavrek, M.A., Elvidge, C.K., DeCaire, R., Belland, B., Jackson, C.D., Brown, G.E., 2008. Disturbance cues in freshwater prey fishes: do juvenile convict cichlids and rainbow trout respond to ammonium as an 'early warning' signal? *Chemoecology* 18, 255–261.
- Verzijden, M.N., ten Cate, C., 2007. Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biol. Lett.* 3, 134–136.
- von Frisch, K., 1938. Zur Psychologie des Fisch-Schwarmes. *Die Naturwissenschaften* 26, 601–606.
- Wisenden, B.D., 2014. Chemical cues that indicate risk of predation. In: Sorensen, P.W., Wisenden, B.D. (Eds.), *Fish Pheromones and Related Cues*. John Wiley & Sons Inc, Ames, pp. 131–148.
- Wisenden, B.D., Dye, T.P., 2009. Young convict cichlids use visual information to update olfactory homing cues. *Behav. Ecol. Sociobiol.* 63, 443–449.
- Wisenden, B.D., Keenleyside, M.H.A., 1992. Intraspecific brood adoption in convict cichlids: a mutual benefit. *Behav. Ecol. Sociobiol.* 31, 263–269.
- Wisenden, B.D., Keenleyside, M.H.A., 1994. The dilution effect and differential predation following brood adoption in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Ethology* 96, 203–212.
- Wisenden, B.D., Mammenga, E.A., Storseth, C.N., Berglund, N.J., 2014. Odour tracking by young convict cichlids and a mechanism for alloparental brood amalgamation. *Anim. Behav.* 93, 201–206.
- Wisenden, B.D., Sargent, R.C., 1997. Antipredator behaviour and suppressed aggression by convict cichlids in response to injury-released chemical cues of conspecifics but not to those of an allopatric heterospecific. *Ethology* 103, 283–291.
- Wisenden, B.D., Stumbo, A.D., Self, P.A., Snekser, J.L., McEwen, D.C., Wisenden, P.A., Keenleyside, M.H.A., Itzkowitz, M., Brisch, E., 2015. Co-evolution of offspring antipredator competence and parental brood defense in convict cichlids. *Hydrobiologia* (in press).
- Wyatt, T.D., 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. *J. Comp. Physiol.* 196, 685–700.