CHAPTER

5.1

Communication in Blennies

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INTRODUCTION

Animal communication was traditionally viewed in a dyadic perspective (signaller—receiver dyad), where the evolution of signals and of perceptual systems relied on the fitness consequences for the sender and receiver (Dawkins and Krebs, 1978; Krebs and Dawkins, 1984). Under this perspective, 'true communication' occurs when signal detection is beneficial for both senders and receivers, 'manipulation' when signal detection is only beneficial for the sender, and 'exploitation' when only the receiver gains by detecting the signal (Bradbury and Vehrencamp, 1998). However, this has been recognised as a simplistic approach to understand communication systems and their evolution, since wherever signals travel further than the average spacing between two individuals, there is a

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potential for a communication network to exist, including the provision of information to unintended receivers (McGregor and Peake, 2000; McGregor, 2005). Therefore, true communication can be defined as the provision of information by a sender who produces a sensory stimulus or signal to one or more receivers that then respond in a way that is beneficial to both sender and receivers. In this case, signallers and receivers form a mutualism in which signals co-evolve with the sensory biology of receivers. Once established, mutually beneficial communication relationships could be susceptible to deceitful manipulations by signallers, which reduce the receiver fitness, and signal interception by unintended receivers (including predators and conspecifics), the response of which to the stimulus may impose fitness costs to the sender (see Searcy and Nowicki, 2005, for insightful discussion).

How do Fish Communicate?

Fish have radiated to all aquatic habitats and consequently evolved an extraordinary diversity of morphologies, relative development of the sensory systems and behaviours. A parallel diversity of communication systems is also expected. However, probably due to the technical difficulties of studying fish in their natural environment, our current knowledge about fish communication systems is limited and probably overlooks its diversity and sophistication. Nevertheless, enough empirical evidence shows that fish in general use the largest number of sensory modalities, including hearing and vision, mechanical (low-frequency vibrations detectable by the lateral-line system), electric and chemical modalities in their interactions with one another (reviews in Ladich *et al.*, 2006a, b; Rosenthal and Lobel, 2006).

COMMUNICATION IN BLENNIES

Combtooth blennies (Blenniidae) form the largest family of true blennies (suborder Blennioidei), and include more than 300 species of, typically, scaleless demersal marine fishes, living in intertidal and subtidal zones all over the world (Zander, 1986; Nelson, 1994). Males are generally larger than females and have a variety of secondary sexual characteristics, especially during the breeding season (Zander, 1975, 1986; Papaconstantinou, 1979). Such secondary characteristics include crests on the head (e.g., *Salaria* spp.), enlarged supra-orbital tentacles (e.g., *Aidablennius sphynx* and *Parablennius* spp.), colour markings on the head and/or body, club-like glands on the tips of the soft rays of the dorsal, caudal and anal fins (e.g., *Microlipophrys* spp.) and glands on the anal fin close to the urogenital opening (e.g., *Salaria* spp. and *Parablennius* spp.). Blennies are poligynandric (i.e., both sexes are variable in their mate numbers in a breeding season, but males are more variable than females) and their general breeding pattern involves males defending a territory where females deposit adhesive eggs in the inner surface of a cavity (crevices, holes, empty shells, or other nesting cavities), and where parental care is given exclusively by the males, guarding the eggs until they hatch (Gibson, 1969; Wirtz, 1978; Almada and Santos, 1995). In some species, alternative male mating tactics (parasitic males) have been described (Santos, 1985b; Ruchon *et al.*, 1995; Gonçalves *et al.*, 1996; Oliveira *et al.*, 2001b; Neat *et al.*, 2003).

Communication has been studied with respect to visual and olfactory sensory modalities in the context of reproductive behaviour. Studies on communication using other sensory modalities are very scarce or absent, but its use by blennies cannot be discarded. An initial study on sound production by Tavolga (1958) describes courtship sounds emitted by males *Chasmodes bosquianus* in aquaria, but this was not followed up by further studies on the same species. Recently, De Jong *et al.* (2007) described the acoustic behaviour of the rock-pool blenny *Parablennius sanguinolentus parvicornis*, in nature. Males produce a grunt-like call when a female approaches and is inside their nest; the call, the variation of which is related with male size, may affect the ultimate decision of a female to spawn and its emission (occurrence and rate of emission) may express some male mate preference (De Jong *et al.*, 2007).

This chapter reviews the available evidence on how and why blennies communicate, focusing on visual and chemical communication in reproductive behaviour. Since communicating is ultimately an integrated process from a behavioural and cognitive perspective, and partitioning communication by modality is only a useful heuristic tool, we will discuss the possible use of multimodal signals between males and females. Finally, the potential for communication networks in chemical and visual communication of blennies is explored with respect to how, in conjunction with other selective pressures, it may have shaped the evolution of their communication mode.

COMMUNICATION USING VISION

Vision in Blennies

A general model describing vision in blennies is difficult to establish for two reasons. First, the properties of visual systems are mainly the result of species-specific adaptations to environmental light and lifestyle and, thus, it is difficult to establish general properties for visual systems based only on phylogenetic relationships. As an example, among four species of Lake Malawi cichlids, there is a strong variation in spectral sensitivity due to differential expression of primarily only three of the seven available cone opsin-coding genes (Parry *et al.*, 2005). Opsins are proteins that are partially responsible for visual spectral sensitivity and the interspecific divergence in their expression pattern—in spectral sensitivity—is probably the result of species differences in both behaviour and environmental light conditions. Likewise, given the fact that the behavioural repertoire of blennies is both rich and diverse and that its members have a widespread distribution, occupying habitats with variable light conditions, it can be predicted that the properties of their visual systems reflect this diversity. Second, although vision has been extensively studied in fish (reviewed in Douglas and Djamgoz, 1990), particularly in some families (e.g., Cichlidae, Salmonidae), it has been poorly studied in blennies. Despite these limitations to establish a general pattern for the visual system, a brief overview of the available data on blennies' vision is presented.

Similar to other fish living in shallow waters, blennies are assumed to make extensive use of vision and, thus, to have a well-developed visual system. This is supported by histological analyses of their retina. Species investigated so far were found to have a fovea or *area* in the retina, i.e., a region with a high concentration of photoreceptors (Kahmann, 1934; Rochon-Duvigneaud, 1943; Collin and Pettigrew, 1988a, b). These regions are associated with increasing visual acuity and, like in most other benthic fishes, they are located in the medial or dorso-temporal retina, allowing for high visual acuity forward and downward (Kahmann, 1936). Blennies living in low-light environments (*Blennius ocellaris* at depths between 10 and 400 m and the cave-dwelling *Microlipophrys nigriceps*) have larger eyes and larger cone outer segments in order to increase the sensitivity of the photonic system, i.e., to decrease the light threshold level necessary for cone-based vision (Zaunreiter, 1990). In contrast, shallow water blennies seem to have smaller eyes and higher cone densities (Zander, 1972; Zaunreiter *et al.*, 1985; Zaunreiter, 1990), presumably having a higher visual acuity. In addition, some intertidal species have evolved adaptations for aerial vision. For instance, the supratidal blenny *Alticus kirkii*, has a *cornea propria*, a structure separated from the anterior part of the cornea and connected to the lens, which defines an additional eye chamber that can be extended by contracting the lens, thus, allowing a further adjustment of the focal point during aerial vision (Zander, 1974).

In 14 species of Mediterranean blennies, the retina contains rods, single cones and paired cones arranged in a regular mosaic (Zaunreiter *et al.*, 1989). This arrangement is typical of species that greatly rely on vision for their lifestyle (Wagner, 1990). The presence of several cone classes usually predicts the occurrence of different photopigments, thus creating the potential for colour vision. Accordingly, multiple cone photopigments have been found in the two blenny species studied so far, the shanny, *Lipophrys pholis* (Loew and Lythgoe, 1978) and the peacock blenny, *Salaria pavo* (White *et al.*, 2004). In the shanny, apart from a rod photopigment, microspectrophotometry has revealed three cone photopigments sensitive to short, mid and long-wavelengths (Loew and Lythgoe, 1978). The spectral sensitivity of the peacock blenny was studied using both microspectrophotometry and behavioural methods. In this species, the lenses exhibit a short-wavelength cut-off (<400 nm) and, unlike the shanny, short-wavelength sensitive photopigments were not detected in the retina (White *et al.*, 2004). The difference in cone classes between these two species may relate to differences in their retinal cone mosaics. The cone mosaics of blennies have paired cones and single central cones and, in some species, accessory single cones (Ali and Anctil, 1976). *S. pavo* lacks the accessory single cones (Zaunreiter *et al.*, 1985) which are, possibly, the short-wavelength sensitive cones of *L. pholis* and other blennies. The lack of short-wavelength sensitive cones and the presence of an ultra-violet cut-off filter in the lens of *S. pavo* is surprising, as these blennies present several bluish spots in the body and an iridescent blue eye-spot in the head that reflect both in the blue and in the ultra-violet part of the spectrum (M. Cummings, D. Gonçalves and R.F. Oliveira, unpublished data). However, measures of spectral sensitivity using the optomotor response showed that *S. pavo* was able to detect wavelengths in the bluish part of the spectrum, possibly using the mid-wavelength sensitive cones which have a wide response spectrum (White *et al.*, 2004).

From the above examples, and keeping in mind the previously mentioned limitations on drawing general properties of visual systems, it seems that blennies have well-developed visual systems of high sensitivity and acuity, capable of colour discrimination and movement detection, as predicted by Kotrschal (1999). Interspecific variation in the visual system may be related with behavioural and lifestyle differences as also with the light properties of their particular environments.

Visual Displays in Blennies

Studies from an ethological perspective show that blennies have complex and stereotyped sexual and agonistic behaviours, and that there is significant interspecific variation in their rich repertoire of visual displays. Therefore, rather than trying to establish general behavioural patterns, examples are given illustrating the diversity of visual displays in blennies.

Most male blennies establish reproductive territories around a crevice or hole in the substrate—which is used as a nest—and undertake aggressive displays against intruding males and courtship displays towards females. In some species, males exhibit conspicuous swimming behaviours in the water column, which may signal their territories to females and other male competitors. These displays include the 'vertical loop swim' of *Istiblennius zebra* (Phillips, 1977), the 'hovering swim' of *Parablennius pilicornis* (Denoix, 1984), or the 'loop swimming' of *P. sanguinolentus parvircornis* (Santos, 1985a). Intertidal blennies living in more turbulent environments do not display in the water columns, instead displaying by head movements like 'nodding' or 'lateral head displays', usually associated with an increase in intensity of head- and body-colour markings, with the male partially inside the nest (Abel, 1964; Zander, 1975; Papaconstantinou, 1979; Almada *et al.*, 1990; Almada and Santos, 1995; Gonçalves and Almada, 1998).

Agonistic interactions may include ritualised threatening displays such as 'lateral displays' (male erecting the unpaired fins and showing the flank to the opponent, and may show lateral turnings of the head), 'undulation swings' (males slowly undulate their bodies from the front to the back), or 'horizontal loops' (male swim around in front of the opponent in a horizontal circle) (Gibson, 1968; Phillips, 1977; Almada *et al.*, 1983; Santos and Barreiros, 1993). In some species, e.g., *S. pavo* (pers. obs.) and *Hypsoblennius brevipinnis* (Losey, 1976), males and sometimes females may turn on, within seconds, an agonistic coloration during aggressive displays. Submission to opponents may also be signalled with visual displays that involve retracting the unpaired fins and lowering the body towards the substrate, and may also include lateral body rotations like the 'lateral presentation' of *P. sanguinolentus parvicornis* males (Santos and Barreiros, 1993). Often, submission postures are accompanied by a general lightening of body colours like in *Hypsoblennius* spp. (Losey, 1976).

In general, males take the initiative in courtship while females adopt a more passive role. Males usually leave the nest and perform conspicuous behaviours towards the female such as 'circling', '8-figure swimming', 'zig-zag swimming', 'lateral body jerkings' or 'quivering' (Fishelson, 1963; Phillips, 1977; Patzner *et al.*, 1986; Santos and Barreiros, 1993). During these displays, males can turn on a nuptial coloration within seconds. As an example, male *S. pavo* increase the conspicuousness of dark bars in the head, crest and chin as the yellow background becomes more intense, with blue spots and lines in the body also increasing in conspicuousness (Patzner *et al.*, 1986).

Females may also exhibit courtship displays. For instance, *S. pavo* females can display to nest holders by presenting their belly while flicking the pectoral fins and rapidly open-and-closing the mouth in synchrony (Patzner *et al.*, 1986). During these displays, females turn on a conspicuous nuptial coloration that consists of vertical dark stripes contrasting with a light background throughout the body (Fishelson, 1963; Patzner *et al.*, 1986). In some populations of *S. pavo*, female courtship is more common than male courtship due to ecological constraints. In the Ria Formosa (southern Portugal), nest sites are scarce and females compete for the access to nesting males, taking the initiative in courtship and playing the major role during sexual interactions (Almada *et al.*, 1995). In contrast, in an Adriatic population, where nest sites are abundant, males display more courtship acts than females (J. Saraiva, D. Gonçalves and R.F. Oliveira, unpublished data). These results suggest that both males and females adjust their visual displays according to ecological settings.

Male blennies may also display to other males in a sexual context. In *P. sanguinolentus parvicornis*, small males achieve parasitic fertilisations of the eggs either by sneaking into the nest of territorial males (i.e., bourgeois males *sensu* Taborsky, 1997) during spawning events or by helping in territory defence and gain a privileged access to the nest during spawning episodes (Santos, 1985b; Oliveira *et al.*, 2001a). In *S. pavo*, small males reproduce using a different strategy. These males have a female-like morphology, and mimic female courtship and nuptial coloration in order to approach the nests during spawning events and parasitically fertilise the eggs (Gonçalves *et al.*, 1996). As discussed below, the occurrence of female-mimics is likely to have a strong impact on male and female courtship displays and, potentially, on the properties of sensorial systems.

In summary, the examples described above clearly demonstrate that blennies make extensive use of visual displays to communicate reinforcing the idea that vision is well developed in this group.

COMMUNICATION USING OLFACTION

Pheromones and Their Detection

Pheromones are molecules (single or in a mixture) released to the environment that cause specific and adaptive physiological and behavioural responses in conspecifics (Stacey and Sorensen, 2002). Vertebrates, in general, release a wide range of different molecules, from relatively small volatile compounds to water-soluble peptides, which are involved in a multitude of different social behaviours such as finding and identifying a mate, regulating the level of aggression and social dominance, mediating the recognition of kin and non-kin, and triggering of alarm reactions (Wyatt, 2003; Kikuyama *et al.*, 2005; Brennan and Zufall, 2006).

In fishes including the Cyclostomata (hagfish and lamprey), there has been growing evidence for water-soluble compounds acting as pheromones and playing a role in all the above-mentioned varieties of social behaviours, as well as in migratory behaviour (Liley, 1982; Wisenden and Stacey, 2005; Rosenthal and Lobel, 2006; Stacey and Sorensen, 2006; Barata *et al.*, 2007). However, with a few exceptions, the chemical structures of the compounds involved remain largely unknown. In many teleosts, reproductive hormones (steroids and prostaglandins) and/or their metabolites released through the urine and/or gills act as hormonal pheromones inducing dramatic changes in the reproductive behaviour and physiology of receivers (Stacey and Sorensen, 2006 and references therein). Other chemical classes of compounds have also been shown to function as sex pheromones in a few fish species. In masu salmon, *Oncorhynchus masou*, L-kynurenine (a major metabolite of the amino acid L-tryptophan in vertebrates) is released through the urine of mature females and acts as a male-attracting pheromone (Yambe *et al.*, 2006). In sea lampreys, *Petromyzon marinus*, males release large amount of bile acids through the gills, which act as sex pheromones attracting females at long distances (Li *et al.*, 2002, 2003; Siefkes *et al.*, 2003). Also, a mixture of sulphated sterols from sea lamprey larvae functions as a migratory pheromone for the adults (Sorensen *et al.*, 2005).

Behavioural and physiological responses to pheromones are mediated by the olfactory system that is, in general, well developed in fishes (for a recent review of the olfactory system, see Zielinski and Hara, 2007). The olfactory organ is a paired structure located in nasal or olfactory cavities located on the dorsal surface of the head to the *rostrum*. The anatomy of the olfactory organ varies across fish taxa, reflecting also differences in lifestyle and behaviour. However, in general, a few or several lamellae, each bearing the olfactory epithelium, form an olfactory rosette located in the bottom of the olfactory cavity; in addition, certain fish have accessory or ventilation cavities which mainly aid in directing the water in and out of the nasal cavity (Zeiske *et al.*, 1992; Kasumyan, 2004).

Receptor cells (sensory neurons) in the olfactory epithelium are of two main types, ciliated and microvillous cells, and a third less abundant type, the crypt cells. These three cell types have clear structural differences and seem to detect different classes of chemical stimuli (Kasumyan, 2004; Zielinski and Hara, 2006; Hamdani and Doving, 2007; Hamdani *et al.*, 2008). Axons of all receptor cells join into the olfactory nerve that conveys olfactory information to paired olfactory bulbs that are the primary olfactory centres for information processing. The olfactory information is further relayed to secondary centres in the telencephalon by the olfactory tract and information causing different behavioural responses (food search, alarm reaction, sexual behaviour) is carried by different nerve fibres (Hamdani and Doving, 2007 and references therein). In the telencephalon, the olfactory information is thought to be integrated with other sensory modalities resulting in appropriate physiological and behavioural responses.

To the best of our knowledge, the olfactory system of blennies has not been studied. Preliminary observations in *S. pavo* females using scanning electron microscopy indicate the presence of two olfactory lamellae bearing ciliated, microvillous and, possibly crypt cells, and a well-developed ventilation sac in each nasal cavity (J. Araújo, O. Lopes and E.N. Barata, unpublished data).

Pheromones in Blennies

The involvement of pheromones in the reproduction of blennies has been hypothesised for a long time. One of the first empirical studies was by Losey (1969), who showed that water conditioned by sexually active conspecifics (males and females) attracted sexually active males in three *Hypsoblennius* species. Glandular complexes on the fins of male blennies were thought to be the source of the putative pheromones (Eggert, 1931; Wickler, 1957; Losey, 1969; Blüm, 1972). Further empirical evidence was obtained by Laumen *et al.* (1974), showing that administration of mammalian luteinising hormone to *S. pavo* males induces size-increase in the glands on the first two anal-fin rays (anal glands), and that fully developed anal glands are a source of putative pheromones effective in attracting females. Later, Lahnsteiner *et al.* (1993) showed that the testicular blind pouches (tubular evaginations of the spermatic ducts) of male blennies, which do not function as sperm reservoirs, secrete steroid glucuronides during the breeding season, and speculated that such compounds could act as pheromones by analogy with the black goby (*Gobius niger*) and the African catfish (*Clarias gariepinus*) (see Patzner and Lahnsteiner, this book). The mesorchial gland of the black goby (Colombo *et al.*, 1980) and the seminal vesicle of the African catfish (Resink, 1987; Resink *et al.*, 1989) produce large amounts of steroid glucuronides which have been suggested to act as sex pheromones that attract females.

Only recently, further progress was achieved on the issue of male pheromones in blennies by making use of behavioural and endocrinological assays combined with the recording of the electro-olfactogram to identify chromatographic fractions of male-conditioned water and anal glands containing putative pheromones. Clearly, the anal gland of male blennies is a source of a sex pheromone that attracts reproductive females from a distance (Barata *et al.*, 2008; Serrano *et al.*, 2008a), thereby enhancing male reproductive success (Barata *et al.*, 2008). In *S. pavo*, each of the two anal glands is a highly folded glandular epithelium containing numerous clusters of secretory cells. These cells differentiate during the breeding season in response to rising plasma-levels of androgens (11-ketotestosterone from the glandular region of the testis—testicular gland) and produce neutral mucins (glycoproteins) (Serrano *et al.*, 2008b, c). Furthermore, the clusters of secretory cells likely produce highly hydrophilic compounds (mostly smaller than 500 Da but may include also compounds larger than 10 kDa) that are odorants for females and may constitute the anal gland pheromone (Serrano *et al.*, 2008a).

The odorants produced by anal glands seem to be different from those derived from hormonal pheromones described in other fishes, and may include amino acids and/or peptides that could be related with mucins produced by the secretory cells. Whether the anal gland pheromones of male blennies are water-soluble peptides or other type of hydrophilic molecules, production of pheromones together with mucous would imply a sustained slow release of sex pheromones for attracting females from a distance to the nesting site throughout the breeding season (Serrano *et al.*, 2008a).

In addition to the anal gland pheromone, sexually mature *S. pavo* males release to the water less hydrophilic compounds which are odorous to the females. These odorants may be responsible for arresting reproductive females in the vicinity of the sending male and, thereby, act as sex pheromones (Serrano *et al.*, 2008a). Although further research is needed, these putative pheromones may originate in testicular accessory organs, i.e., blind pouches and/or testicular glands that are a source of potent male odorants for females (Serrano *et al.*, 2008c) and may include steroid glucuronides. The steroid maturation hormone 17,20β-dihydroxy-4-pregnen-3-one and its sulphate and glucuronide conjugates, and the androgen 11-ketotestosterone are excluded as possible candidates since the olfactory system of females is not sensitive to neither of these sex hormones (R.M. Serrano, P.C. Hubbard and E.N. Barata, unpublished data) which are hormonal pheromones in other teleost species (see Stacey and Sorensen, 2006 and references therein).

A multi-component male pheromone, comprising different compounds of different physiological origin, provides chemical information to the females, the effect of which in their reproductive behaviour may depend on the distance to the sending male (Serrano *et al.*, 2008a, b, c). The anal gland pheromones may disperse through long distances and convey information to females about species identity and location of potential mates. At close distance from the male in its nesting site, putative pheromones from the testicular accessory organs, especially the blind pouches, may arrest the females in the vicinity of a male that is likely to fertilise the eggs and invest in parental care. The mixture of anal-gland and gonad pheromones may affect female's ultimate decision to spawn.

The hypothesis of a multi-component male pheromone in *S. pavo* requires further studies on the chemical identities of male odorants and their effect on female reproductive behaviours. However, given that all combtooth male blennies studied so far have testicular blind pouches (Patzner and Lahnsteiner, 1999; Richtarski and Patzner, 2000; Patzner and Lahnsteiner, this book) and glands on the fins (either anal glands or club-like glands on the tips of rays in the several fins) (Northcott and Bullock, 1991 and references therein), it is reasonable to predict that multi-component pheromones may be widespread in this fish group.

It is unknown whether *S. pavo* males also respond to male pheromones or if females produce pheromones that could affect the behaviour of males or females. In the black goby, which has a mating system similar to that of combtooth blennies, territorial males respond aggressively to putative pheromones from conspecific males but parasitic males are pheromonally inconspicuous (Locatello *et al.*, 2002).

Evolution of Chemical Communication

As noted first by Døving (1976), hormonal products are pre-adapted to serve as pheromones because they are produced and released at relevant times (Stacey and Sorensen, 2006). Indeed, several teleost species use reproductive hormones and/or their metabolites as reproductive pheromones and its use is thought to be widespread among teleosts (Stacey and Sorensen, 2006 and references therein). Although senders can have some control as to the timing, context, and quantity of release of hormonal pheromones, e.g., accumulation and release *via* the urine (Appelt and Sorensen, 2007), remains to be determined in most cases to what extent waterborne hormones are acting as pheromonal signals, rather than as pheromonal cues incidentally released by reproductive individuals.

Evolution of true chemical communication (pheromonal signals) would be expected when individual donors improve their reproductive success due to change(s) in the way they produce and/or release a pheromonal cue (Stacey and Sorensen, 2006). However, sex hormones function endogenously in senders; therefore, their function as a pheromonal signal seems to be constraint by their function as hormones. Consequently, evolution of sex pheromone signals in teleosts would require strong selective pressures (e.g., sexual selection) imposed by receivers upon senders which in turn would find ways to specialise their release of pheromones; e.g., through increase of diversity, amount and water-solubility of sex steroid metabolites released to the water by specialised cells and/or differentiation of external glands under control of key sex hormones, that would produce and secrete specialised chemical compounds.

Sexual selection is a selective pressure that likely has been operating in the evolution of blennies' reproductive behaviour and may have driven the evolution of their putative multi-component pheromone system. The androgen 11-ketotestosterone (presumably from the testicular gland) is a key hormone that organises the production of putative pheromones from the anal gland and testicular blind pouches (Serrano *et al.*, 2008c) and is positively correlated with the expression of parental/bourgeois male behaviour (Oliveira *et al.*, 2001c, d). Therefore, the hypothesised multi-component male pheromone reflects accurately the physiological condition of a male and can convey reliable information to females about the location of a conspecific mate that is likely to fertilise the eggs and invest in parental care (i.e., fanning and guarding the eggs). Consequently, female reproductive success may have been an important driving force for the evolution of the proposed chemical communication system. In addition, a possible role of male-male competition in shaping this evolutionary process cannot be excluded.

MULTIMODAL COMMUNICATION

Communication is ultimately an integrated process from a behavioural and cognitive perspective. Although communication is partitioned by modality as a useful heuristic tool of study, the outcome of the process integrates several sensory modalities. For example, to track an odour source, Banded kokopu (*Galaxias fasciatus*) use hydrodynamic cues detected by the lateral line system rather than bilateral comparison of olfactory stimuli (Baker *et al.*, 2002). In the Mozambique tilapia (*Oreochromis mossambicus*), males use both visual displays and chemical signals released via the urine to advertise their aggressive motivation and social status (Barata *et al.*, 2007) and in the cichlid *Pseudotropheus emmiltos*, both chemical and visual information are necessary for recognition of conspecific males (Plenderleith *et al.*, 2005).

In blennies, since visual, olfactory and apparently, acoustic signals are sent by males, there is potential for females to use various sensory modalities in their reproductive behaviour. Although male pheromones seem to play no role in triggering female courtship which is exhibited in close visual contact with a nesting male in *S. pavo* (Gonçalves *et al.*, 2002), the relative importance of different sensory modalities can change with the context or distance to the sender. At long distance without the male in sight, the anal gland pheromone may lead the female to a closer distance and then—together with putative pheromones from the testicular blind pouches—the full pheromonal 'bouquet' may arrest the female in the vicinity of the potential mate. Furthermore, at close distance visual and pheromonal signals may reinforce the male's features causing a step further, e.g., female courting the male and entering the nest. Finally, acoustic signals may also be involved in final steps of choosing the mate given their apparent importance in the reproductive behaviour of male blennies, as suggested by De Jong *et al.* (2007).

In the peacock blenny (*S. pavo*), females exert mate choice by choosing larger males with a larger head crest, anal gland and genital papilla, that have more eggs in the nest and court females (Oliveira *et al.*, 1999; Fagundes *et al.*, 2007). Pheromones from the anal gland seem to be crucial in female mate-choice, at least when eggs are not present in the nest (Barata *et al.*, 2008). Also, it has been suggested that females use a 'one-step decision' in searching for mates, i.e., females mate with males that satisfy an adjustable threshold criterion, balancing the quality of the mates expected to find in the next step of the search and the effort of finding them (Fagundes *et al.*, 2007). Therefore, the use of several sensory (e.g., vision and olfaction) modalities to assess mate quality (i.e., likelihood of egg fertilisation and efficient paternal investment) may increase the amount of information gained and decrease the time or energy spent on male assessment by females. Moreover, multi-component signals may also aid in discriminating males and in recognition through associative learning. For reviews on the use of multi-component signals in animal communication, see Rowe (1999), Candolin (2003), Partan (2005) and Harper (2006).

In summary, the reproduction of blennies seems to involve communication using multiple sensory modalities and multi-component signals within a sensory modality. However, more empirical evidence is necessary to make generalisations and understand the consequences that the use of multiple signals may have in the process of sexual selection and speciation in blennies.

COMMUNICATION NETWORKS

Signals may travel distances large enough to be detected by third parties and thus are usually available for several receivers simultaneously (McGregor, 1993; McGregor and Dabelsteen, 1996; Peake, 2005). The concept that animals typically communicate in networks (involving at least one signaller and more than one receiver) and the ecological and evolutionary consequences of such networks have been explored thoroughly for visual, acoustic and chemical signals by McGregor (2005). Wisenden and Stacey (2005) have discussed the chemical communication networks in fishes. Here, some general predictions on the evolution of fish signals and sensory systems will be presented under the conceptual framework of communication networks and hypothesis will be drawn with respect to communication networks in blennies.

Eavesdropping refers to 'the use of information in signals by individuals other than the primary target' (Peake, 2005). Eavesdropping may have costs for both senders and receivers. For example, the interception of courtship signals by parasitic males can have negative fitness consequences for both the bourgeois male and the female. For the bourgeois male because egg fertilisations can be lost for the parasitic male, thus decreasing its own reproductive success; for the female either because bourgeois males will decrease parental investment when the probability of paternity decreases and/or because larger bourgeois males can offer higher genetic benefits to females than small parasitic males (see Taborsky, 1999). At this point, it is useful to make a distinction between species where the parasitic males are morphologically distinct from females and reproduce by sneaking or darting into the nest and species where parasitic males are similar to females.

In species with morphologically distinct parasitic males, the females and bourgeois males are expected to be able to detect them and should evolve inconspicuous signals, i.e., 'conspiratorial whispers' (Dawkins and Krebs, 1978; Maynard Smith, 1991; Johnstone, 2000), or adjust their signalling behaviour when the parasitic males are in the vicinity in order to decrease the probability of their signals being intercepted. For instance, in the Mediterranean wrasse *Symphodus ocellatus*, bourgeois males decrease courtship displays towards females when the number of parasitic males is experimentally increased and the reverse occurs when the number of parasitic males is decreased (van den Berghe and Warner, 1989; Alonzo and Warner, 1999; 2000). Likewise, females of this species prefer to spawn when parasitic males are absent, increasing their spawning rate several fold when parasitic male were experimentally removed (van den Berghe and Warner, 1989; Alonzo and Warner, 2000). Thus, when the parasitic males are morphologically distinct from females and impose costs on both the bourgeois male and the female, courtship signals are expected to be inconspicuous or not to be displayed in the presence of eavesdroppers, and parasitic males are expected to counteract by evolving strategies and perceptual systems that favour signal interception.

In the case of female-mimicry, different predictions can be drawn. In these species, parasitic males reproduce by mimicking females in order to approach the nests of bourgeois males and achieve parasitic fertilisations of the eggs. Thus, female-mimics rely on deception to reproduce and it can be predicted that bourgeois males will be under a strong selective pressure to discriminate females from female-mimics. Females, on the other hand, are expected to gain by signalling to the males that they are females and not female-mimics in order to be accepted into the nest. This could lead into an increase in the complexity of female displays in order to difficult its mimicry by parasitic males. Because parasitic males rely on female-mimicry to reproduce, an evolutionary arms race between the females and the female-like male displays is predicted (Dawkins and Krebs, 1979).

In blennies, female-mimicry has only been described for *S. pavo* (Gonçalves *et al.*, 1996). Small males (sneakers), with higher gonadosomatic index than bourgeois males, reproduce by mimicking female morphology and behaviour, and sneaking fertilisation of eggs during spawning events (Gonçalves *et al.*, 1996; Oliveira *et al.*, 2001e). Sneaker males have lower plasma concentration of androgens than the nesting males (Oliveira *et al.*, 2001b) and do not differentiate the anal gland. Interestingly, this species presents one of the most elaborated female courtship displays described in blennies. It is unknown whether this is a consequence of the predicted evolutionary arms race between females and female-like males, or of selective pressure imposed by the perceptual system of bourgeois males, or both. Small sneaker-males size-matching females are able to deceive bourgeois males as these direct an equivalent proportion of courtship and aggressive acts towards females and sneakers (Gonçalves *et al.*, 2005). However, with increasing body size of the sneakers, the efficacy of female-mimicry seems to decrease as bourgeois males direct more aggressive acts and less courtship displays towards these males when compared with females of the same size (Gonçalves *et al.*, 2005). Presumably, and considering that bourgeois males should be under a strong selective pressure to discriminate females from female-like males, larger parasitic males are easier to discriminate from females but the cues used by bourgeois males to achieve this have not been identified.

Also, sneaker males are more sensitive to longer wavelengths than both bourgeois males and females (White *et al.*, 2004). Whether this relates to the different behavioural tasks that bourgeois males, females and sneaker males need to accomplish remains to be tested.

In addition, although not tested yet, what can be predicted is the eavesdropping of sneaker males on the chemical communication between bourgeois males and females in order to find the bourgeois males more attractive to females. This may also impose a selective pressure shaping the elaboration of the chemical signal from bourgeois males, the perceptual system of females to male chemical signal and the male's perceptual system to possible odours from conspecifics.

Eavesdropping can also confer fitness advantages to both senders and receivers, although this is less intuitive. In some species, the females copy the mate choice of other females by observing which males are chosen by other females (Dugatkin, 1992). Thus, a high quality male (i.e., a male that is usually chosen by the females) should gain by exhibiting conspicuous signals that favour eavesdropping by other females. The primary female, i.e., the female being directly courted by the male may also gain by having other females eavesdropping on the interaction. For example, in some fish species, the males provide more or better parental care to the eggs when the number of eggs increases (Coleman *et al.*, 1985). The primary female can gain direct benefits in terms of increasing male parental care over her eggs by having its courtship interaction eavesdropped by other females. In such a scenario, female and male courtship signals should be conspicuous and promote eavesdropping. Presently, no empirical evidence is available to support this hypothesis in blennies.

Finally, eavesdropping can have different fitness consequence for senders and receivers and thus generate conflicts between them. For instance, in the bitterling *Rhodeus sericeus*, females increase the fertilisation success of their eggs if sneakers participate in spawning (Smith and Reichard, 2005). Thus, females perform conspicuous behaviours in order to increase eavesdropping probability and participation in spawning by sneakers (Smith and Reichard, 2005). Bourgeois males, however, decrease their reproductive success when sneakers participate in spawning e.g., *Lepomis punctatus* (Dewoody *et al.*, 2000) and, thus, are expected to avoid eavesdropping. This creates a conflict between females and males. In this case, both male and female sexual signals result from a compromise between costs and benefits for both. Males may reject or punish females that solicit spawning with signals above a certain threshold, as this would attract eavesdroppers, and females may not respond to males that display below a certain threshold, as this would not attract eavesdroppers. A similar argument can be predicted for situations where eavesdropping favours males but has costs for females. In the above example on female copying, males may gain by having the interaction intercepted by other females but the primary female may suffer costs from attracting other females (for example, egg fertilisation rate may be lower if other females participate in spawning). Again, male and female signals are expected to result from an evolutionary compromise between the sexes.

In summary, communicating in a network has evolutionary consequences for signal and perceptual systems design. Fish are not an exception and the properties of their signals and sensory systems are best understood in the evolutionary context of communication networks. However, there is still a long way to go in order to fully understand the proximate and ultimate causes of communication in fish and especially in blennies.

SUMMARY AND CONCLUSIONS

The scarcity of studies limits the validity of generalisations on how and why blennies communicate. However, it is clear that blennies use signal and perceptual systems involving hearing, vision and olfaction for communication in the context of their reproduction.

Very little is known about sound production and reception in blennies, since there is only one study showing that male rock-pool blennies produce grunt-like calls during courtship which may play a role in female spawning decision.

Vision is clearly important in blennies as they have well-developed visual systems with interspecific variation that may relate to behavioural and lifestyle differences. Moreover, males have visual features clearly distinct from females and there is great intra- and interspecific variation in the rich repertoire of courtship and agonistic visual displays of blennies, reinforcing the idea that visual communication is important in their reproduction.

Female blennies use their sense of olfaction to detect male odours that originate in external epidermal glands and testicular accessory organs, the production of which depends on androgen plasma levels in correlation with the seasonal development of males' reproductive organ. These odours are putative sex pheromones, likely comprised of a mixture of different chemical compounds, which attract females and may affect their mating decision. However, only the peacock blenny has been studied. Therefore, establishing the general use of pheromones in blennies and how and why pheromones are involved in their reproduction requires additional studies with more species and chemical identification of the active compounds.

In conclusion, communication using multiple sensory modalities is involved in the reproduction of blennies. Females may use vision and olfaction to find males in their nesting sites and integration of visual, olfactory and acoustic signals from males may affect their ultimate decision to spawn; the relative importance of different sensory modalities affecting female reproductive behaviour may change with the context and/or distance to male signallers. Communication within sexes and eavesdropping on signalling systems has not been studied. Clearly, proximate and ultimate factors underlying communication deserve further attention in order to understand how and why blennies, as well as fish in general, communicate to achieve their reproduction.

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