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Communication and Competition in Fish

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Doctoral Thesis

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DECLARATION

I declare that given Ph.D. thesis is solely my own work unless otherwise referenced or acknowledged.

Prague, 13th of July 2017

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PROVERB

This thesis is submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy in the Czech University of Life Sciences Prague and consists of four research chapters published in research journals.

Fourth research chapter reviews a number of studies dealing with olfactory sensitivity and highlights the need of proper knowledge of physiological and behavioral background in animal research. Although it is not a study focused on fish behavior, it also deals with intraspecific communication and therefore was included into this thesis.

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COMMUNICATION AND COMPETITION IN FISH

1 COMMUNICATION

Most of the interactions between individuals among animal kingdom involve communication. Starting with caterpillar warning bright colors, ends by vocal communication at a distance of kilometers in elephant. What is in common for all communication is special signals that are features of one individual (signaler) causing behavior changes of another (receiver) (Dawkins and Krebs, 1978; Smith and Harper, 1995). Communication is adaptive in a variety of social context because it conveys information. Signalers would not produce signals if it would not be beneficial for them, and receivers would not respond to them if it would not be beneficial for them (Seyfarth and Cheney, 2010). Social interactions significantly influence animal behavior through sensory perception (Chen and Fernald, 2011). The efficacy of signal transmission consists of a complex interaction between signal production, traits of the signal, environmental properties and signal processing by receiver sensory systems (E. Hebets, 2011). Communication distance (active space) is influenced by environmental complexity like habitat structure (Rundus and Hart, 2002), light environment (Rosenthal, 2007), substrate seismicity (Uetz et al., 2013).

The information which signal is conveying plays the crucial role in signal shaping. The stimuli specificity differs among signals (broad array stimuli versus high specific stimuli) (Seyfarth and Cheney, 2017), for example general alert calls and predator-specific calls in

mammals (Manser, 2001). The signal specificity e. g. how easy it is to distinguish a particular signal from other signals in repertoire of a producer shapes design of a signal as well (Naguib and Price, 2013). Animals can gain very definite information from even not very precise signal incorporating information from the context in which the signal is emitted (Searcy et al., 2014). Environmental constraints (dense forest, long distances, aquatic environment) shape signal's modality and form. Also the social context (intraspecific versus interspecific) plays an important role in signal design (Laidre and Johnstone, 2013a).

A trade-off in communication occurs when intended and unintended receivers are present as greater detectability may increase the cost of signaling by attracting eavesdroppers such as competitors or predators (Roberts et al., 2007).

Also learning determines communication process. With experience, animals acquire information about the relationship between their reaction and particular outcome (Seyfarth and Cheney, 2017) The internalization of contextual information is crucial when having a history of interaction and recognizing each other (Booksmythe et al., 2010). Experience about another individual is memorized in fish. Such a behavioral history cause individual brain changes (Desjardins et al., 2010).

1.1 SIGNALS

In a broad definition, a signal is an aspect of a signaler that affects behavior of a receiver. We can divide signals into static (coloration, body size) and dynamic components (sound, movements). Sensory capabilities are important for decision-making in social behaviors as shoaling, competitive encounters, mate selection or courtship (Laidre and Johnstone, 2013).

Visual signals during interspecific interactions evoke changes in behavior (Chen and Fernald, 2011) and play decisive signaling role in many fish species (Kocher, 2004). Fish focus light onto retina using large spherical lens where it is detected by rod and cone photoreceptors (Rowland, 1999). Typically there are multiple cone types containing different visual pigments (Pignatelli et al., 2010). In cichlids, visual communication is critical among others for competitive behaviors and mate choice (Seehausen and Schluter, 2004; Selz et al., 2014), although it may be supplemented with other cues such as acoustic (Amorim and Almada, 2005) or olfactory (Thünken et al., 2014). Cichlid species differ significantly in visual sensitivities, even among closely related species, as cichlids have seven different cone opsins (O'Quin et al., 2012) and are adapted to the light transmitted in different environments (Hofmann et al., 2009). In some cichlid species, lens also absorbs UV light and these spectral properties depend on the light-rearing environment (Kröger et al., 2001). Coloration is an

important dominance indicator in fish. In some species, such as salmonids pale (O'Connor et al., 1999; Suter, 2002) or bright coloration (Höjesjö et al., 2007) signal dominance status whereas in others, such as cichlids, dark coloration mediates information about superiority (Beeching, 1995; Oliveira and Almada, 1998a; Volpato et al., 2003). Catfish in general are not orientated by visual cues, not even in laboratory light condition, which suggest catfish to orient mainly by other senses (Pohlmann et al., 2001).

Acoustic communication during agonistic encounters and during reproductive behavior was observed in numerous fish species (Myrberg and Fuiman, 2002; Amorim and Almada, 2005; Ladich and Schulz-Mirbach, 2016; Myrberg and Fuiman, 2002). In fish, there are two pathways of sound detection. Sound can be transmitted through delayed movement of the otoliths and hair cells after (Popper and Fay, 2011) or through indirect stimulation of swim bladder transmitting energy to endolymph and otoliths, and hair cells similarly (Schulz-Mirbach et al., 2013). The sound production mechanism involves sound generation by the pharyngeal mill, amplified by swim bladder (Kaatz and Stewart, 2012). A variety of acoustic signals is an important part in intraspecific communication in cichlids (Amorim et al., 2003). Sounds are produced during aggressive (Raffinger and Ladich, 2009) and reproductive interactions (Lobel, 2001). In cichlids, acoustic communication is typical for about 20 species but only males emit sound during territory defense (Bertucci et al., 2010) and courtship (Ripley and Lobel, 2004). Acoustic signals in cichlid fish are broadband grunts with various peaks across situations (Smith and Van Staaden, 2009). Pulse period and number of pulses of courtship sounds are significantly different depending on behaviors they are associated with (Amorim et al., 2003). However, high tolerance for temporal structure modulations was found in cichlid species with no effect of pulse period and number of pulses on behavioral response (Bertucci et al., 2013). Acoustic signals also are population-specific creating geographically differentiated dialects (Danley et al., 2012). Species-specific differences have been found in closely related cichlid species and courtship calls may play an important role in species recognition (Amorim et al., 2008). Territory holders have higher androgen levels and show more of mating behavior toward females (Oliveira and Canário, 2000). Dominant males that achieved to defend their territories elicit significantly more acoustic signals than defeated subordinate males (Amorim and Almada, 2005). They elicit pulse acoustic signals of low-frequency to attract females and to activate gamete release (Amorim et al., 2003). Acoustic signals convey information about emitter's quality as larger males produce longer pulse duration and greater amplitude modulation (Bertucci et al., 2012). Only territorial males exhibit quivering accompanied with sounds, whereas sneaking males quiver without emitting

sounds (Oliveira and Almada; 1998c). Territorial males respond to acoustic playbacks by increase of territorial activity (Bertucci et al., 2013). European catfish was found to have a responsive sense of hearing (Popper and Fay, 2011) and to produce courtship sound seasonally (Alp et al., 2004).

Chemical senses are closely interconnected in aquatic organism (Giaquinto and Volpato, 1997). Olfactory organ in fishes is located in the nasal cavity, in multi-lamellar rosette. Olfactory epithelium with olfactory sensory neurons is directly exposed to aquatic environment (Hansen and Zielinski, 2005). Gustatory cells with taste buds are located in the oral cavity, pharyngeal cavity, gills, fins, and skin in some fish species (Kasumyan and Doving, 2003). Aspects of the chemical sensory neurons vary with ecology and foraging habits (Huber et al., 1997).

Social cognition is based on olfactory cues in many fish species (Ladich, 2000) as well as in cichlids (Giaquinto and Volpato, 1997; Thunken et al., 2009) and catfishes (Pohlmann et al., 2001). Cichlid olfactory sensitivity serves to recognize conspecifics (Blais et al., 2009; Plenderleith et al., 2005) and detect their social (Barata et al., 2007; Hubbard et al., 2014) and reproductive status (Miranda, 2005; Keller-Costa et al., 2015). Olfactory signals convey information about dominance status in territorial males (Oliveira and Almada, 1996). The amount of androgens excreted in urine serves as signal of individual's fighting ability (Almeida et al., 2005; Barata et al., 2007). In catfish Siluriformes, chemical receptors are densely distributed on the whole body surface and barbels (Atema, 1971). Chemical senses, olfaction and taste, are important to pursue moving and non-moving prey in European catfish *Silurus glanis* (Linnaeus, 1758; Pohlmann et al., 2001).

Mechanosensory system is an ancient sensory system in all fish species (Montgomery et al., 1995). Mechanosensory lateral line system detects unidirectional and low frequency oscillatory water flows and plays critical role in prey detection and other behaviors (Montgomery et al., 2009). Mechanosensory system consists of neuromast receptor organs located on the skin and in pored lateral line canals (Webb et al., 2014). Neuromasts are sensory structures of groups of hair cells stimulated by oscillatory fluid flow (Webb, 1989). Cichlids are able to discriminate low frequencies by lateral line (Mogdans and Nauroth, 2011) and two types of lateral line canals can be found within this fish family (Webb et al., 2014). Some cichlid species are generally considered to be visual predators whereas others detect their prey by water flows (Butler and Maruska, 2016). In poor lighting conditions living European catfish *S. glanis* is a typical predator (Boujard, 1995) orientated by mechanosensory system (Pohlmann et al., 2001).

Passive electroreception detects weak bioelectric fields in aquatic environment (Whitehead and Collin, 2004) through ampullary pores distributed over the entire body of the fish, but in higher concentrations in the head region (Whitehead et al., 2003). This ancient sensory modality was found only in three orders of teleost fishes including Siluriformes. European catfish *S. glanis* are able to detect dipole-like electric field that surrounds fish bodies (Whitehead et al., 2000).

Some vertebrates orientate over long distances using magnetic field of the Earth, but the sensory system behind this perception remains unclear. Magnetoreception was found in fish especially in migratory species and was verified in Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852; Walker et al., 1997).

1.2 SIGNAL HONESTY

In many cases signaler and receiver have conflicting interests thus signaling in this case might be more manipulative than informative (Krebs et al., 1984; Laidre and Johnstone, 2013). Therefore signals given during conflicting encounters will be evolutionary stable only if they are costly (Zahavi, 1975) and lying would have negative consequences greater than benefits (Adams and Mesterton-Gibbons, 1995). However, when signalers don't gain anything by deceiving honest signals don't need to be costly and *Cheap talk* can evolve (Silk et al., 2000). Low-cost signaling is particularly likely to evolve when individuals are interested in the same outcome (non-escalated competition) (Seyfarth and Cheney, 2017). According to the *Handicap principle*, reliability of fighting ability displays is enforced by signal costs, or handicaps. Animals of better abilities can better afford to pay these handicap costs, which can lower abilities animals not afford (Johnstone and Grafen, 1993). Fighting ability cannot be exaggerated therefore fighting ability displays are honest signals and cannot be faked (Reby et al., 2005). In dyadic contests of convict cichlids *Archocentrus nigrofasciatus* (Günther, 1867) fighting ability displays are decisive factor in contest outcome (Leiser et al., 2004).

Under specific conditions, bluffing by animals of low fighting ability can persist as a profitable tactic (Adams and Mesterton-Gibbons, 1995). Scaling the *Handicap principle*, communication systems in which threats do not impose handicaps are subject to bluffing, which also leads to elimination of receivers response (Alan Grafen, 1990). Alternatively, communication systems may consist of a mix of reliable and deceptive signals (Adams and Caldwell, 1990). Deception is costly for receivers to inspect signaler to distinguish bluffing from honest signals. Since the advantage of bluffing and inspection are frequency dependent, deception persists as long as it is at a sufficiently low frequency (Dawkins and Guilford,

1991; Grafen and Johnstone, 1993). Such deceptive signals can be found in anglerfish *L. piscatorius* (Linnaeus, 1758) that uses lure to attract other fish to prey on (Laurenson and Priede, 2005) or in mantis shrimp *Gonodactylus bredini* (Manning, 1969) displaying by spreading out forelimbs even with molted exoskeleton (Adams and Caldwell, 1990).

1.3 MULTIMODAL SIGNALING

A sensory system within a signal produced by the signaler and perceived by a receiver is referred to as modality. Signals can consist of one or more cues perceived together as a signal (Uetz and Roberts, 2002). If cues benefit to different sensory modalities then the signal is considered as multimodal (Candolin, 2003). *Multimodal signals* are produced and detected by two or more sensory systems (Otovcic and Partan, 2010). Multiple signals belonging to the same modality detected by same sensory system are commonly referred to as *multicomponental signals* (Quinn and Hews, 2010). Moreover we can also find *multicomponental multimodal signals* combining multiple signals within a sensory modality with signals from other modalities (Smith and Evans, 2013).

Signals that consist of more than one modality are more likely to exceed receiver's detection threshold and increase the probability to be perceived (Candolin, 2003). It is often the interaction between two modalities that determines the signal function and efficacy (Smith and Van Staaden, 2017). Multimodal signaling may have evolved to compensate environmental and social constraints on transmission of signals (Wilgers and Hebets, 2011) as different modalities presented together increase active space of a signal and thereby the probability of a signal to be detected (Uetz et al., 2013). Multimodal communication is advantageous because of assessing multiple sensory inputs versus just a single modality provides more accurate information. In a noisy environment more multimodality may be needed for efficient communication (Pohl et al., 2009). However it is difficult to distinguish how different sensory modalities are integrated and processed (Hebets and Papaj, 2005). Vibratory signals are more likely to be detected in close range, while farther away, visual signals are more likely to be seen (Uetz et al., 2013). Multimodal signaling varies considerably within close related species, as some species uses a single mode, whereas related species uses more modes (Hebets and Uetz, 2000; Uetz and Roberts, 2002).

But the flexibility in signal production as reaction to environmental noise in multimodal communication is not well-studied (Ernst and Banks, 2002; Partan, 2013). There is a lack of knowledge in variation within and between signals in different modalities to signal function and signal efficacy and interaction between environment and modalities of a signal (Smith

and Evans, 2013). Large gap of knowledge in multimodal communication might be solved by development of novel experimental techniques such as computer manipulation, which might offer potential future insights (Uetz and Roberts, 2002).

In teleost fish, sound production is often accompanied by visual signals (Myrberg and Fuiman, 2002). Acoustic threat displays are accompanied with visual displays in aggressive encounters in fish, whereas different sound types could be distinguished for different situations during competition (Ladich, 2000; Raffinger and Ladich, 2009). Behavioral variability in signaling is important in determining how communication channels are extended (Van Staaden and Smith, 2011).

Multimodal signaling in cichlid fish was, in context of other species, conclusively described long since (Silverman, 1978; Tavolga, 1974). Within their diversity of complex behaviors, cichlids are a useful subject for studying multimodal pathways of communication (Smith and Van Staaden, 2017). Visual communication is well studied whereas the role of other communication modalities receives less attention (Van Staaden and Smith, 2011). Visual cues might be the most important component in multiple signaling. However, behavioral experiments revealed that vocalization and olfaction may be required for correct behavioral answer (Blais et al., 2009; Smith and Van Staaden, 2009; Verzijden et al., 2010). Sound production during courtship is accompanied by quivering behavior, but quivering may also occur without any sound (Ripley and Lobel, 2004). Courtship sound accompanies a specific behavior to more clearly denote the intentions of the signaler (Amorim et al., 2003). Female cichlids favor males using vocal and visual cues over males using only visual displays (Maruska et al., 2012). In multimodal test of courting behavior visual cues alone led to lowered behavioral reaction than unlimited cues (Blais et al., 2009). Competition studies have shown that fishes are unlikely to respond to agonistic sound stimuli alone (Raffinger and Ladich, 2009), but adding visual stimuli to acoustic stimuli increases behavioral response in agonistic encounters (Plenderleith et al., 2005). No behavioral response to acoustic playbacks was found when they were not accompanied by visual stimuli (Bertucci et al., 2012). This suggests visual displays to be key signals for courtship interactions (Estramil et al., 2014). There also might be a hierarchy among sensory modalities depending encounter succession (Simões et al., 2008), Olfaction may be important for close-range communication already initiated on the basis of visual signals, less often on the basis of acoustic signals (Hubbard et al., 2014). Lateral displays typical for cichlids (McElroy and Kornfield, 1990), might be multimodal as low frequency audio stimuli might be detected as mechanosensory with lateral line system (Montgomery et al., 2009).

2 COMPETITION

Most of their lifetimes, animals are involved in competitions for different resources - food territory, or mates. Competing about resources costs energy and increases the risk of an injury or death (Turner and Huntingford, 1986). Many factors interact to determine the course, duration and outcome of a contest as well as behavior of contestants (Arnott and Elwood, 2009). The most important factors influencing competition outcome are body mass, body condition, weapon size, previous experience, and resource value (Archer, 1988; Riechert, 1998). The intrinsic (body size and condition, weapon size) (Enquist and Leimar, 1983; Umbers et al., 2012) and extrinsic factors (previous experience, resource value) (Leimar and Enquist, 1984; Enquist and Leimar, 1987) must be integrated together, but relative little is known, how component factors scale in by forming fighting behavior (Hsu et al., 2006) and it is difficult to distinguish between the single factors (Enquist et al., 1990; Sacchi et al., 2009; Smith et al., 1994). Competition outcome might also be influenced by other factors as hunger (Stocker and Huber, 2001) or injuries (Taylor and Jackson, 2003). But in experimental competition studies these factors are usually eliminated.

Survival success is based on proper evaluation of costs and benefits (Parker and Rubenstein, 1981; Arnott and Elwood, 2009). Animals, in general, assess the costs and benefits associated with contests and adapt their fighting behavior to this assessment (Yuying Hsu et al., 2006). Fighting costs are minimized by assessment of each other's fighting potential, which avoid heavily unmatched contests (Albon and Clutton-Brock, 1979).

Assessment models are crucial to understand agonistic interaction mechanism and competitive behavior (Reichert and Gerhardt, 2011). Numerous theoretical models explain decision-making processes during contest describing how competitors decide about energy they spend on competing about resources (Dugatkin and Mesterton-Gibbons, 1996; Kokko, 2013; Mesterton-Gibbons and Heap, 2014). We can distinguish two assessment approaches in general. In *Self-assessment model* individual's costs and benefits alone determine contest decisions. According to *Self-assessment theory*, an individual should retreat when ratio between its own costs and benefits reaches a certain threshold (Briffa and Elwood, 2009). Competitors do not assess rivals' fighting abilities directly, but persist until the costs of competition reach a threshold limit based on their own fighting abilities (Bridge et al., 2000; Prenter et al., 2006; Stuart-Fox, 2006). On game theory based *Sequential assessment model* implements ratio between fighting abilities of two competitors into decision models (Enquist

et al., 1990; Taylor and Elwood, 2003). However, in competition observations it is difficult to discriminate between models (Pratt et al., 2003).

2.1 RITUALIZATION

When competing for limited resources (food, territories, mates), individuals often use sequences of visual (Leiser et al., 2004), acoustical (Raffinger and Ladich, 2009) and/or chemical (Keller-Costa et al., 2015) signals to assess each other's fighting ability. Rather than immediately moving onto escalated fights, competition consist more likely of ritualized fighting ability displays (Beeching, 1992; Keeley and Grant, 1993). Different agonistic behaviors serve *Sequential assessment* (Koops and Grant, 1993; Payne, 1998), as there is a correlation between individual's fighting ability and its aggressive signaling (Briffa and Elwood, 2000; Lyons and Morris, 2008). Based on this assessment individuals decide to retreat or escalate conflict (Leiser et al., 2004). A dyadic competition can also be viewed as type of *War of attrition* (individuals trade off strategic gains from outlasting others and the real costs expended with passage of time, Maynard Smith, 1974) where the outcome of a contest is determined by willingness of both contestants to participate (Hammerstein and Parker, 1982). *Energetic war of attrition* predicts contest duration to be determined by maximum cost, that weaker individual is willing to invest (Mesterton-Gibbons et al., 1996; Payne and Pagel, 1996). This was confirmed by studies, where expectation of higher pay off tends to prolong or escalate the contest and increase winning probability (Enquist and Leimar, 1987; Olsson, 1992; Wells, 1988). When potential costs are expected to be high because of large size of an opponent, for example, individuals tend to retreat sooner (Enquist et al., 1990; Turner, 1994).

In number of fish species, males show ritualized sequences of visual signaling referred to as *Visual display* (Leiser et al., 2004). *Visual display* provides information about relative size and fighting abilities of contestants (Keeley and Grant, 1993). It serves faster winner determination (Neat et al., 1998; Payne, 1998) and prevents injuries of both rivals (Brick, 1999; Hardling et al., 1999). Ritualized visual signaling appears mainly in the beginning of a competition and, compared to escalated physical fights, energetic costs are relatively low (Neat et al., 1998). *Visual displays* rarely escalate into physical fights and most contests are settled by *Sequential assessment*, however when size asymmetries between rivals are low displaying can lead to escalated fight anyhow (Koops and Grant, 1993; Maan et al., 2001). In poeciliid, agonistic behavior rarely evolves into escalated physical encounters. Escalated fighting only occurs when two similar-sized males are confronted (Bisazza et al., 1996). In

brown trout *Salmo trutta* (Linnaeus, 1758), a short interval is sufficient for assessing mutual fighting abilities reliably (Höjesjö et al., 2007). In cichlid *Nannacara anomala* (Regan, 1905), order of *Visual displays* in a contest is very consistent, with constant rates of single behaviors for each phase (Jakobsson et al., 1979). In cichlid *O. mossambicus* dominance hierarchy in a group is already established after few hours (Oliveira and Almada, 1996). *Visual displays* are main component of dyadic conflicts, by whose males provide information about their fighting abilities to each other (Leiser et al., 2004; Oliveira and Almada, 1999).

2.2 RESOURCE VALUE

In social species, dominance hierarchy determines distribution of limited resource such as territory, food, shelter or mating partner. Dominant individuals have priority in resource access (Huntingford et al., 1990). Limited resources usually are high valuable objects of rivalry and increase aggression between individuals (Sultana et al., 2013). Dominant individuals obtain territories of better quality with more food and shelter resources available (Imre et al., 2004). Territories with large number of shelters are highly valued (Johnsson and Akerman, 1998). Shelter value increases with increasing predation risk (Johnsson et al., 2004). Game-theoretical models propose contest duration and intensity to be positively correlated with *Resource value* (Hurd, 2006). *Resource value* is directly related to resource abundance (O'Connor et al., 2015) and it changes seasonally according to availability of the resource (Sultana et al., 2013). Resource abundance is expected to be negatively correlated to resource value as the resource value increase with decreasing resource availability (Keeley and McPhail, 1998; Toobaie and Grant, 2013). Food deprivation or limited mating opportunities increase *Resource value* (Keeley and Grant, 1993). Hungry brown trout *S. trutta* are more aggressive and compete about resources more vigorously than fed conspecifics (Johnsson and Björnsson, 1994; Johnsson et al., 1996). In round goby *Neogobius melanostomus* (Pallas, 1814), males compete more aggressively about closed than open shelters and previous experience with the resource is required to assess the *Resource value* efficiently (McCallum et al., 2017).

Resource value plays an important role in contest duration and outcome (Olsson and Shine, 2000) and fighting intensity (Lindström, 2001). Subjective assessment of *Resource value* is also linked to previous ownership of a resource (Beaugrand et al., 1996; Petersen and Hardy, 1996). Therefore *Resource value* may exceed other competition factors such as individual fighting ability (Riechert, 1998) however, in other competition studies *Resource value* seems

to be of limited importance influencing contest duration and intensity (Sherratt and Mesterton-Gibbons, 2015).

2.3 RESOURCE HOLDING POTENTIAL

Resource holding potential is defined as a measure of fighting ability (Parker, 1974) and it is a crucial factor in agonistic interactions. Competition outcome depends upon competitors absolute and relative *RHP* (Briffa, 2008). In case that all factors are equal, individual with higher *RHP* has higher chance to win the contest (Haley, 1994), as higher *RHP* individual is willing to incur higher costs (Beaugrand et al., 1991). *RHP* can be assessed exclusively on basis own fighting abilities evaluation (*Self-assessment*) or relative to the rival (*Sequential assessment*). Duration of a contest is determined by give up decision of one of the contestants (Taylor and Elwood, 2003). When *RHP* asymmetries are large, contestants are able to assess these differences and are able to solve competitive encounter using displaying and ritualized behaviors without escalation and physical interactions (Arnott and Elwood, 2009). When *RHP* asymmetries are small, fight takes longer and is also more intensive (Enquist et al., 1990; Marden and Rollins, 1994; Riechert, 1998). Also when there is inaccurate information about *RHP* asymmetries it can lead to an escalated conflict (Smith and Parker, 1976).

2.4 BODY SIZE

Among the most important factors that can influence duration, intensity and outcome of a contest body size and weight seem to play crucial role (Riechert, 1998; Smith and Harper, 1995). According to *Resource holding potential* term originator Parker (1974), body size is identified as a crucial *RHP* factor in animal conflicts. *RHP* is closely related to competitor's body size as large individuals are more likely to win physical escalated contests (Briffa, 2008; Reichert and Gerhardt, 2011) and body size is generally related to fighting success (Archer, 1988). As body size correlates naturally with strength it is a determining factor for conflict outcome in fish (Beaugrand, 1997; Nijman and Heuts, 2000; Prenter et al., 2008). Larger individuals are bolder (Ashley et al., 2009), more active (Candolin and Voigt, 2001) and are more willing to forage under predation risk (Gotceitas and Godin, 1991). Large individuals distinctively attack smaller individuals more frequently than vice versa (Cutts et al., 1999) and become dominant (Kokko et al., 2006; Umbers et al., 2012). In aquaculture, larger individuals are automatically the more dominant ones (Brzeski and Doyle, 1995; Seppa et al., 1999). In numerous studies where body size is a decisive factor in contest outcome large size difference increase the probability that larger opponent wins (Benson and Basolo, 2006; Briffa and Sneddon, 2007), especially when contest escalates to physical attacks (Briffa and Elwood,

2005; Reichert and Gerhardt, 2011). In stealhead trout *Salmo gairdneri* (Richardson, 1836) competing about food resources, size difference smaller than 6% decides the competition outcome in favor of larger individual (Abbott et al., 1985). In cichlids, larger opponent wins competition (Draud and Lynch, 2002) even when the size difference is less than 5% of body size (Keeley and Grant, 1993). Even when size asymmetries are small, larger individuals win conflicts. Only in case size asymmetries are minute, smaller fish can achieve a win (Prenter et al., 2008).

Size difference between rivals might be also a predictor of contest duration (Enquist and Leimar, 1983; Marden and Rollins, 1994). When size difference between two rivals is bigger fights are expected to be shorter (Taylor and Elwood, 2003) and less escalated (Hack, 1997; Riechert, 1998). When smaller individual assess fighting costs as too high, it retreats (Turner, 1994). But when the size differences are minute it can also happen that larger individual assess asymmetries inaccurately and retreats first (Smith et al., 1994). Larger male is more likely to win, and with very big difference in size smaller fish give up more or less immediately in cichlid *Nannacara anomala* (Jakobsson et al., 1979; Enquist et al., 1990). In cichlid *A. nigrofasciatus*, when body size asymmetries are the same, contest duration is of the same length in pairs of large males as in pairs of small males. However in pairs of large males more *Visual displays* and longer fight latency occur (Leiser et al., 2004). Same principle was found also in other cichlid species (Turner and Huntingford, 1986; Keeley and Grant, 1993; Neat et al., 1998). In large individuals, escalated fight might lead to serious consequences. This might be the reason why large males spend more time displaying (Turner, 1994).

Body size is directly linked to body weight, which is an important fight duration factor (Archer, 1988; Riechert, 1998; Taylor and Elwood, 2003). With increasing body weight asymmetry contest duration is correspondingly decreasing (Riechert, 1998). With increasing body mass subordinate individuals are willing to take high-risk strategies (Turner, 1994; Hack, 1997; Bridge et al., 2000; Taylor and Elwood, 2003).

However, in some studies large body size does not obviously bring an advantage in competition (Marden and Rollins, 1994; Kemp and Wiklund, 2001). An advantage of large body size may be counterbalanced by greater agility of small males (Bisazza et al., 1996). Males in poorer condition might be more aggressive as obtaining another source is difficult for them (Just and Morris, 2003) or they have less to lose (Just et al., 2007).

Competitive interactions are usually not decided by one trait. When two competitors are symmetrical in one trait, asymmetry of another trait seems to decide competition outcome (Beaugrand et al., 1996; Eshel and Sansone, 2001; Kokko, 2013). There are other measures

related to individual's *RHP*, such as energetic state or body condition (Briffa and Elwood, 2005; Prenter et al., 2006), as displaying and fighting is energy demanding (Kemp and Wiklund, 2001). Moreover are these factors highly correlated with individuals body size (Reichert and Gerhardt, 2011). Energetic state and body condition may be exceeded by weapon size when it comes to physical fights but also to visual displays only (Barki et al., 1997; Sneddon et al., 1997). In swordtail fish *Xiphophorus helleri* (Heckel, 1848), sword size has a significant effect on the contest duration (Royle et al., 2006). Time loser needs for giving up is influenced by the size of winner's sword relative to its body size. A relative large sword is a substantial advantage for faster winning (Prenter et al., 2008). Although the sword is not used as a weapon in contest (Basolo and Wagner, 2004) it is associated with better swimming and therefore fighting abilities or it can be simply explained as condition indicator (Royle et al., 2006). Other immeasurable intrinsic components play role in contest outcome determination (Beaugrand et al., 1996), such as inner motivation (O'Connor et al., 2015), aggression (Barlow et al., 1986) or mating readiness (Leiser et al., 2004). *Gonadosomatic index* calculates testicle size of a male individual relative to its body size. *GI* is proved to be an important dominance indicator in cichlid *Tilapia zillii* (Gervais, 1848; Neat et al., 1998) and *O. mossambicus* (Oliveira and Canário, 2000). As the amount of androgens excreted in urine provides information about hierarchy dominance bladder size might also be additional competition factors in *O. mossambicus* (Keller-Costa et al., 2015).

Territorial quality correlates with male traits (Johnsson et al., 1996; Leiser et al., 2004). In sticklebacks *Gasterosteus aculeatus* (Linnaeus, 1758), the largest males defend the biggest territories (Candolin and Voigt, 2001). In brown trout *S. trutta*, size of defended territory also correlates with resident's body size (Johnsson and Björnsson, 2001). Moreover, dominant territory holders grow faster than subordinate intruders, which might be the partial reason for larger males obtaining bigger territories (Weber and Fausch, 2003). Also nest size is positively correlated with males' dominance in *O. mossambicus* (Oliveira and Almada, 1996).

2.5 EXPERIENCE

Shortly after a competition, winners and loser show physiological changes (Winberg et al., 1992) that differs in steroid hormones levels (Cardwell and Liley, 1991). These physiological changes substantially influence contest behavior and energy invested in subsequent competitions (Haller, 1991; Neat et al., 1998; Overli et al., 1999). Experience can also influence mating readiness in competing males (Amorim and Almada, 2005).

Experience from previous competitions referred to as *Winner and loser effect* is termed as non-RHP-related factor of contest outcome (Mesterton-Gibbons et al., 1996). Competition outcome generally depends on the costs-benefit expectation in both rivals (Hsu et al., 2006). *Winner and loser model* hypothesizes prior winning and losing experience to influence individual's assessment of its own RHP and therefore estimation of cost-benefit ratio (Beaugrand and Beaugrand, 1991; Hsu and Wolf, 1999; Koops and Abrahams, 2003). In general, prior winning experience increases, whereas prior losing experience decreases winning probability in subsequent contest (Hsu et al., 2006). Winning experience influences contest duration and outcome as it increases self-perception of individual's RHP (Dodson and Schwaab, 2001; Dugatkin and Earley, 2004). It also increases willingness to invest energy and to escalate fight (Thorpe et al., 1995). Especially when size or weight asymmetries are minor prior winning experience is a decisive advantage in favor of previous winner (Beacham and Newman, 1987).

Naive contestant does not have precise knowledge about rival's RHP (Jennings et al., 2004), potential costs and benefits (Koops and Abrahams, 2003) or about resource quality (McCallum et al., 2017). Information from previous competition seems to reduce contest duration and intensity (Hammerstein and Parker, 1982; Höjesjö et al., 2007). However previous experience becomes less important in contests with escalated physical fights (Hsu et al., 2009).

In *Oncorhynchus mykiss* (Walbaum, 1792), previous experience of by-standing observer settles subsequent conflict faster and with less aggression (Johnsson and Åkerman, 1998). Dyadic experiments in swordtail fish *X. helleri* suggest prior experience and body size to be main competition factors and to have additive effect in competition outcome. Body size effect determines the conflict outcome mainly when opponents have equivalent prior experience (Beaugrand et al., 1996). Prior subordinate experience can be outweighed only by pronounced superiority in body size. An individual with a losing experience has to be weight superior (100%) to outcompete an individual with winning experience. When the weight asymmetries are relative small (20-40%) prior dominance experience cannot compensate the weight disadvantage (Beaugrand et al., 1991). Moreover in comparison of an isolated fish with a fish with previous experience, isolated fish behave similar to fish with previous winning experience and outcompete larger opponents with losing experience (Beacham and Newman, 1987). *Winner and loser effect* and body size have additive effect on contest outcome also in blue gourami *Trichogaster trichopterus* (Pallas, 1770). With prior subordinate experience gourami are not able to dominate smaller opponents (10% in body length) (Frey and Miller,

1972). But when the body size asymmetries overcome 80%, body size becomes decisive factor (Beacham, 1988). In steelhead trout *S. gairdneri*, even small body size asymmetries (5%) influence the contest outcome in favor of a larger individual when both contestants have same previous experience. In individual with losing experience not even size superiority (60-110%) compensates for prior submissiveness (Abbott et al., 1985). In pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus, 1758), previous experience is of importance only when size asymmetries are small (less than 40%), in case of bigger size asymmetries previous experience is overweighed (Beacham, 1988). Prior experience must be considered together with other competition factors such as prior residency which is closely related to prior experience as a resident is also a previous winner of a territory contest (Begin et al., 1996; Hsu et al., 2009).

2.6 RESIDENCY EFFECT

Previous ownership or familiarity with the area where competition proceeds referred to as *Residency effect* influences *RHP* and affects competition outcome (Olsson and Shine, 2000; Kemp and Wiklund, 2004). When *RHP* of both contestants is equal, chances of a resident to win are higher than chances of an intruder (Enquist et al., 1990). *Residency effect* is directly linked to *Winner and loser effect* as residents experienced competition win already (Hoeffler, 2002; Goubault and Decuignière, 2012). According to game theory most aggressive individuals obtain territory and based on higher *Self-assessment* they continue to win in subsequent contests (Smith and Parker, 1976; Kemp and Wiklund, 2004). Territory size and value is closely related to fighting abilities of territory holder (Candolin and Voigt, 2001). We can find distinct differences in movement activity between residents and intruders (Cote et al., 2010), reflecting individual motivation differences in resource competition (Humphries et al., 2006; Tricarico and Gherardi, 2007). Resident defends its own territory more aggressively than intruder (Arnott and Elwood, 2009; O'Connor et al., 2015), which might be caused by differences in subjective *Resource value* (Keeley and Grant, 1993; Johnsson and Forser, 2002). Higher subjective *Resource value* leads to increased fight motivation which might overweight individuals low *RHP* (Lindström, 2001). Resident's chances to win are therefore distinctly higher (Jennions and Backwell, 1996; Fayed et al., 2008), as more aggressive individuals obtain the resources more likely (Stuart-Fox, 2006). Residents often initiate fights first which influence the competition outcome in their favor (Umbers et al., 2012). With decreasing *RHP* asymmetries, resident's chances to win increase. In swordtail fish *X. helleri*, when differences between contestants are smaller than 10% of body size,

competition outcome is determined by prior experience with prior winners defeating prior losers (Beaugrand et al., 1996). An intruder can defeat a resident only in case intruders *RHP* outweigh residents *RHP* significantly (Jennions and Backwell, 1996). Prior resident may profit of time it spent in preferred area (Koga and Ikeda, 2010) and of a better position there (Fayed et al., 2008).

In salmonids Salmonidae, prior residency represents a substantial advantage (Johnsson and Forser, 2002). This advantage is obtained by territory holder after only single day of acclimatization (Huntingford and Leaniz, 1997). When there are pronounced body size asymmetries body size was shown to be decisive factor in resident and intruder competition (Rhodes and Quinn, 1999), but when the fish is of similar size, *Residency effect* alone decides which individual obtains the territory in juvenile Atlantic salmon *Salmo salar* (Linnaeus, 1758; Cutts et al., 1999). Residents initiate territorial competition more often than intruders in brown trout *S. trutta* (Deverill et al., 1999). With increasing residence duration territory value increases as well, which lead to increased motivation and to increased probability to defend the territory (Johnsson and Forser, 2002). *Residency effect* is linked to inner motivation which also explains differences in aggression level between monogamous and polygamous cichlids *Neolamprologus pulcher* (Trewavas and Poll, 1952; O'Connor et al., 2015). In cichlid *O. mossambicus*, intruders are defeated by large residents fast and without any escalation into physical fight. But when large intruders encounter small residents fight gets escalated, takes longer and lot of agonistic interactions occur (Turner, 1994). However, in swordtail fish *X. helleri*, large size asymmetries, determine competition outcome and size advantage nullifies other advantages of previous winning or prior residency (Beaugrand et al., 2012).

2.7 FAMILIARITY

Familiarity decreases aggression and stabilizes dominance hierarchy in a group of fish (Höjesjö et al., 1998) improves general fitness and supports growth (Seppä et al., 2001). The ability to distinguish familiar individuals from unfamiliar ones plays a crucial role in cooperation (Chivers et al., 1995; Krause et al., 2000) and effective use of resources (Ward et al., 2007). In general, individuals associate with familiar conspecifics more than with unfamiliar (Croft et al., 2005; Slavík et al., 2012). Association of familiar fish is based on olfactory and visual cues (Krause et al., 1996). Recognition of familiar individuals also determines competitive interactions (Griffiths, 2003; Magurran et al., 2011). When rivals have a previous fighting experience with each other, individual recognition helps to reduce fighting costs in subsequent competitions (Utne-Palm and Hart, 2000; Frostman and Sherman, 2004).

Individual recognition is essential also for stabilizing dominance hierarchies and for reducing aggression among group members (Johnsson and Åkerman, 1998; Hemelrijk, 2000), as repeated encounters reduce fighting intensity (Keeley and Grant, 1993; Miklósi et al., 1997). In a group of familiar individuals level of energy spent is lower as well as number of injuries (Griffiths and Armstrong, 2000; Ward, et al., 2007). Reduced aggression level toward familiar individuals can be explained by *Dear enemy effect* (Fisher, 1954), which is characterized by the fact that competition between resident and familiar neighbor is less aggressive than between resident and unfamiliar intruder. In steelhead trout *S. gairdneri*, individual recognition plays an important role in dominance hierarchy stability. Subordinate fish never become dominant, not even when they grow to a superior body size. However, with the same body size asymmetries in unfamiliar fish, bigger individuals become the dominant ones (Abbott and Dill, 1985). Familiarity plays an important role in reducing aggression in brown trout *S. trutta* as well (Höjesjö et al., 1998). In swordtail fish *X. helleri*, fish re-establish dominance hierarchy based on individual recognition rather than on prior fighting experience (Beaugrand and Zayan, 1985). In European catfish *S. glanis*, social structure is well developed and allows familiar individuals to make more effective group decisions (Slavík et al., 2012). In aquaculture production, fish are usually sorted out according to their body size so a homogeneous group of fish is created (Martins et al., 2005). *Grading* distorts dominance hierarchy and increase the level of aggression among individuals (Martins et al., 2006). In contrived homogenous group of fish individuals have to expend a lot of energy to compete about resources (Stefánsson et al., 2000) and to re-establish dominance hierarchy (Sunde et al., 1998; Slavík et al., 2011). Therefore, *Grading* is one of the most important stress factors in fish aquaculture (Martins et al., 2012). Fish reared in aquaculture and released into natural streams exhibit higher level of aggression for the same reason of missing stable dominance hierarchy (Johnsson et al., 1996).

2.8 COOPERATION

Cooperation is an outcome that is advantageous for the members of group of two or more individuals, and whose achievement requires collective action (Dugatkin and Mesterton-Gibbons, 1996). Cooperation among related individuals has been satisfactorily explained by *Inclusive fitness theory* based on indirect benefit of helping relative individuals and forwarding individuals genes further (Hamilton, 1963). However cooperation is more complicated among unrelated individuals (Dugatkin, 2002).

According to *Prisoner's Dilemma theory*, mutual cooperation yields a higher reward to each than mutual defection does. In fish *Cooperator's dilemma theory* explain three categories of cooperative behavior-reciprocal altruism, group selection and by-product mutualism (Dugatkin and Mesterton-Gibbons, 1996). Reciprocity is based on help because some help back in the future is expected, such as partners exchanging roles by taking care about egg clutches in hermaphrodite sea bass *Hypoplectrus nigricans* (Poey, 1852; Petersen, 2006). By-product benefits are produced by otherwise selfish acts, such as cooperative foraging in wrasse, *Thalassoma lucanum* (Gill, 1862; Foster, 1987). Group selection gives priority to benefit shared by a shoal of fish to the detriment of individual's costs, such as predator inspection in minnows *Phoxinus phoxinus* (Linnaeus, 1758; Pitcher et al., 1986). Cooperation might also be supported by enforcement that rewards cooperation and punishes free riding, such as in cleaner fish *Labroides dimidiatus* (Valenciennes, 1839), that is chased away when biting its client (Bshary and Grutter, 2005). Another issue may be the apparent variability in the propensity of conspecifics to cooperate. Crucial point might be than to gather information about partner's willingness to cooperate (Mesterton-Gibbons et al., 2002) and cooperation may have lot to do with partner choice then (Noë, 2001).

In cichlids, cooperative breeding increases inclusive fitness of helpers (Bender et al., 2008). Group selection was reported in some shoaling cichlid species (Pitcher, 1992). Only juvenile individuals usually form groups in solitary living European catfish *S. glanis* (Boulêtreau et al., 2011) and cooperation and familiarity in this species was scarcely investigated (Slavík et al., 2012).

3 EXPERIMENTAL APPROACH

3.1 COMMUNICATION STUDIES

Understanding of the interaction between two modalities is the subject of interest in number of behavioral studies of animal communication (Smith and Evans, 2013). Interaction can alter signal detectability and signal discrimination (Hebets and Papaj, 2005). It is necessary to quantify the effect of each modality relative to the other to understand the mechanism of animal communication (Smith and Evans, 2013). Two signals may have an additive effect, multiplicative effect, may overshadow or alter the information effect (Partan, 1999). Moreover, combined multimodal signals may elicit unique behaviors (Acquistapace et al., 2002; Narins et al., 2003). Sensory channels can also vary considerably among families, genera and species and there is great interspecific variety in signaling behavior (Uetz and Roberts, 2002). Evaluation of function and information content of multimodal signals is based on receiver responses (Partan and Marler, 2005). Experimental studies examine receiver behavior related to signal components when changing signal production of each modality (Smith and Evans, 2013). In cue-conflict studies, cues of different modes are presented simultaneously. This type of experiment allows determination of whether both modes must be present or whether a specific modality is primary. To observe behavioral response to different stimuli presented simultaneously a choice chamber can be used (Uetz and Roberts, 2002).

The scientific value of the outcome of an experiment is closely related to its design where one of the big categories of concerns is related to problems arising from how the experiment was conducted. Stimulus design, context, and delivery are crucial to a meaningful experiment. These design concerns appear in traditional approaches to investigating visual and acoustical stimuli, e.g. live stimuli, dummies, still photographic images, as well as in playback experiments (McGregor, 2000).

First studies focused on understanding sensory guidance of animal behaviors involved manipulation of sensory organs to isolate different sensory channels (Uetz and Roberts, 2002). For example in order to investigate the importance of acoustic signaling fishes were muted surgically (Ladich, 1997). But the surgically manipulation can distinctly influence behavior. Following studies examined the role of different modalities, alone and together by modification of the perceptual environment of the target stimulus. Investigating the relative importance of single signaling modes several experimental techniques including cue isolation, cue conflict and computer manipulated playbacks are used to tease apart elements of multimodal signaling (Uetz and Roberts, 2002). The most common experimental method

presents unimodal signals separately and compares the behavioral response with response toward combined multimodal signals (Smith and Evans, 2013). In cue isolation, single modalities are switched off, using opaque partitions, non-vibrating materials etc. when separating object and focal individual (Uetz and Roberts, 2002). In fish, the presence and absence of visual (mirror) and acoustical (playback) is used to examine the relative importance of single modalities in agonistic encounters (Raffinger and Ladich, 2009). Many traditional studies using live animals and dummies do not adequately reproduce natural light conditions (Fleishman et al., 1998). Limitations occur using glass or acrylic barriers in live-animals experiments that often filter out the critical parts of the spectrum (Hunt et al., 2001). In live animals experiments as well as in dummies experiments, also a problem about neutral background arises. What background to use to imitate natural color and depth conditions is an important question. In acoustic experiments, stimulus isolation is not a problem as it is often played against a silent background. But there is no similar solution for visual background (Rosenthal, 1999). In many aquatic taxa however, there is often at least a homogenous background in natural condition (Oliveira et al., 2000). There may also be a visual perception effect caused by prolonged exposure to artificial light condition, therefore it is important to rear animals under natural light conditions (Kroger, 2003). Another complication lies in fact that animals often do not express natural color patterns in an artificial environment (Oliveira et al., 2000). However, the last concern might be solved using computer manipulated stimuli.

Computer manipulated stimuli playback is an experimental technique in which natural or synthetic signals are manipulated, broadcasted and behavioral response of focal animal is noted (McGregor, 2000). Computer manipulated stimuli are suggested as suitable technology for assessing behavioral response of various species (Rosenthal, 2000). The approach allows the manipulation of stimulus independently of one another with substantial precision (Oliveira et al., 2000).

Although some behavioral studies show computer animations to be useful and flexible tool in studying visual cues in fish communication (Baldauf et al., 2008; Thünken et al., 2011), experimental success varies substantially between studies (Fleishman et al., 1998; Clark and Stephenson, 1999; Mazzi et al., 2003). The potential confound of interactive behavioral feedback between focal and stimulus individual is usually prevented using this experimental tool which might be one of the reasons (Fleishman et al., 1998). However, there is also number of technical concerns which might influence appropriate use of computer manipulated stimuli. Most concerns are related to technical imperfections (Fleishman and Endler, 2000).

Obviously use of these experimental techniques is limited to the capability of perceiving video and reproduced acoustic cues in particular species (Baldauf et al., 2008). However, visual and acoustical stimuli are extraordinary complex so it is difficult to assume all important aspects of playbacks. Conversion of live stimulus to video causes alternation in perceived appearance of an image, as the video system is designed for human perception. Moreover often in modes experimenter is not able to determine and control (Oliveira et al., 2000).

Computer manipulated stimuli must be constructed with reference to natural light conditions in general (Rosenthal and Ryan, 2000). First, monitor output and ambient illumination must be taken together (Endler, 1993). Second, screen refresh rate corresponds with critical flicker fusion frequency in humans, while in some animals CFFF is higher and the flicker may be distracting for them. Moreover, differences in visual perception are crucial in species with high temporal resolution (birds, insects), which do not perceive apparent motion of video as continuous (D'Eath, 1998). If focal animal is close enough to a monitor and has a high spatial resolution, then it will perceive the image as dots mosaic rather than a continuous image. To choose monitors or screens with the smallest pixel spacing is therefore important for an authentic image (Oliveira et al., 2000). Spatial context also determines behavioral response. Absence of depth cues become a concern as relative size of stimulus object should change with motion. Change in angular size of stimulus object and occlusion gradients may however alleviate depth cue insufficiencies (Zeil, 2000). Photoreceptors absorption spectra vary widely across species with often more than four photoreceptor classes (Hofmann et al., 2009). Video monitors are tuned to the absorption spectra of the corresponding human photoreceptors (D'Eath, 2007) and therefore fail to represent the appropriate colors in many species (Oliveira et al., 2000). Monitors also do not emit the directed ultraviolet light that many animal species can detect (Fleishman and Endler, 2000). Similar lightning limitations occur using glass or acrylic barriers that often filter out the critical parts of the spectrum (Hunt et al., 2001). In cichlid fish, light spectrum is particularly important, especially for shallow water species where substantial UV light penetrates (Hofmann et al., 2009). Taken together, when preparation of visual stimuli is careful, playback might be suitable for studying motion, shape, texture, size, and brightness (Balshine and Lotem, 1998) but studying color might be problematic because video systems are designed for human color perception (Oliveira et al., 2000).

The focal signal often reflects constrains of our ability to manipulate the structure of a particular signal rather than the relative importance of the signal (Smith and Evans, 2013).

Moreover, it is important to be aware that whether the subject can perceive difference in natural stimuli and whether the subject can perceive a difference in video stimulus presented are different issues (Van Staaden and Smith, 2011). There are also other concerns in design and analysis of behavioral experiments such as pseudoreplication, external validity, types of measurements and combination of qualitative and quantitative responses, interpretation of no response differences (McGregor, 2000).

Interactive presentation of signals to live animals might be the most useful of experimental approaches because of the reciprocity of the stimuli (Ord and Evans, 2002). The latest experimental approach of behavioral studies is therefore an alternation of the playback stimuli in response to the behavior of the subject by an investigator in interactive playback experiments of visual (McGregor, 2000) and acoustic communication (Estramil et al., 2014). Not only computer manipulated playbacks but also different types of models and robots in various display postures are used in interactive behavior experiments. Although it seems to be experimental approach of future investigations there are even more methodological concerns in design (reaction of stimulus) and analysis (pseudoreplication) (McGregor, 2000).

Main concern in acoustic playbacks is related to species-specific auditory sensitivity (Ladich and Fay, 2013) and most of the species specific thresholds were measured under laboratory conditions using no additional sound as an acoustic background (Ladich and Schulz-Mirbach, 2013). In natural condition however these auditory thresholds are elevated due to environmental noise such as rain, wind, movements of plants, ships etc. (Kennedy et al., 2010; Wysocki et al., 2007). In laboratory condition environmental noise is usually compensated with white noise (signal of equal intensity at different frequencies) (Wysocki and Ladich, 2005), which also is used as control sound (Estramil et al., 2014). Although sound playback experiments are useful tool for studying relevance of different sound characteristics in many vertebrates, successful playback experiments in acoustic fish species remain rare (Bertucci et al., 2013). Acoustic devices allowing sound playbacks in water are scarce as they do not present low frequency sounds that most of fish species emit appropriately. Further constraints are caused by increased pressure due to water depth. New underwater loudspeakers designed for playback experiments was presented by Fonseca and Alves (2012) allows lowing frequency sounds to be reproduced with high accuracy from about 10 Hz up to 3 kHz, frequency range that fits for purposes of complex sounds playbacks of many fish species (Fonseca and Alves, 2012).

3.2 COMPETITION STUDIES

To investigate how intrinsic and extrinsic factors determine behavior, duration, running and outcome of a contest, competitions studies focused on single factors are examining competitive behavior (Olsson, 1992; Briffa and Elwood, 2009). To understand competition mechanism, all factors must be integrated together, however, relative little is known about how component factors scale in by forming fighting behavior and contest outcome (Hsu et al., 2006).

In the vast majority of competition studies life animals are used to study agonistic behavior. However to use life competitors risk injuries in studied individuals (Abbott and Dill, 1985). Using a mirror in behavioral studies ensures the course of competition without injuries and better clarity of observations and therefore is common in fish (Raffinger and Ladich, 2009). Computer manipulated stimuli are useful tool to investigate competitive behaviors (attacking, displaying) and to observe some of competition factors separately (*RHP*, coloration) (Baldauf et al., 2009, 2010; Verzijden et al., 2010; Thunken et al., 2011). Playback experiments are mostly designed to address questions ultimately related to genetic fitness such as mate choice or resource defense (Oliveira et al., 2000).

Competitive behavior studies led to number of hypothesis taking part on competition running and outcome (among others, Beaugrand et al., 1996; Johnsson and Forser, 2002; Höjesjö et al., 2007). *Resource holding power hypothesis* presumes individual of larger size or better condition to win thanks to its better fighting ability (Smith and Parker, 1976a). *Value asymmetry hypothesis* supposes win to be based on different resource value assessment (Dill, 1983). *Pay-off asymmetry* is closely related to the former hypothesis and predicts resource holder to win as resource value increases over time (Enquist and Leimar, 1987). Theoretical models also predict how the single hypothesis can be integrated together (Mesterton-Gibbons and Sherratt, 2016). Numerous models vary in conclusions depending on which factors are examined. Most studies focus on only one of a number of possible assessment mechanisms without integrating it into overt competitive process. These models would need to be first confirmed experimentally. More carefully controlled experiments of underlying mechanisms are needed before theoretical conclusions (Huang et al., 2011).

Methodological differences may contribute to conclusion difference. For example, the protocol used to offer fighting experience to focal individuals is conducted either with size-matched or self-selected individuals (Begin et al., 1996). There are also methodological differences caused by variation in frequency and duration of previous contest. Fighting experience can last for a relative short period (Hsu et al., 2006) or until winner-looser status is

established (Chase et al., 1994). Differences in time amount focal individuals are allowed to acclimatize, establish its territory or recover from previous experience contribute to different competition outcome as well (Martínez et al., 1994; Hsu et al., 2009). Also, individuals reared isolated are more aggressive than individual reared together (Halperin et al., 1997). The time focal individuals have been separated from original group affects level of aggression and therefore subsequent competition testing (Schuett, 1997; Earley and Dugatkin, 2002). Methodological differences among competitive studies contribute to differences in results. Ideally, standardized procedures should be adopted to facilitate data comparison among studies (Miklósi et al., 1997).

4 EXPERIMENTAL ANIMAL

4.1 MOZAMBIQUE TILAPIA

African cichlid Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) is of great scientific and economic interest due to its use in aquaculture and its rapid invasive propagation (Russell et al., 2012; Sanches et al., 2012).

Mozambique tilapia *O. mossambicus* is a polygynous, socially living cichlid of the lakes and rivers of southeast Africa with distinctive sexual dimorphism. It is a maternal mouth-brooding species, which is breeding in leks (a place where the males gather to attract females) in African lakes and rivers (Bruton and Bolt, 1975). Males are highly territorial and the dominance hierarchy plays a crucial role in the functioning of fish group (Oliveira and Almada, 1996). Male's synchronization of courting behavior seems to be a reaction to female hormone release as a sign for ongoing ovulation (Oliveira and Canário, 2000). At the beginning of the mating season, the males gather together in a lek in shallow waters (Fryer and Iles, 1972) and in sandy bottom they dig out a pit. The pit is aggressively defended against other males, and females are attracted to the pit by territorial males (Oliveira and Almada, 1998a). Territorial males are larger than females and typically black in color (Bruton and Bolt, 1975), black coloration however disappears in seconds when the male is defeated by another territorial male (Neil, 1964). The higher the male stands in the hierarchy of the group, the bigger the nest and it is located in the center of the lek (Turner, 1986). Before females leave the lek area after courtship, they snatch the gametes in their mouths up where they become fertilized. The spawn develop in females mouths for 20-22 days than until it hatches and the fry become free swimming (Bruton and Bolt, 1975). But the females continue to protect their mobile juveniles by collecting them in the case of danger (Oliveira and Almada, 1998b).

Mozambique tilapia *O. mossambicus* is often used as model organism to study bony fish reproduction (Teleostei), due to its endurance, great expansion, highly developed communication, courtship behavior and dominance hierarchy, mainly (Baerends and Baerends-Van Roon, 1950). Various mating tactics were described in this species. Subordinate males can take over the coloration and behavior of females and show mating behavior towards another dominant male (Oliveira and Almada, 1998c), as an attempt to fertilize a bunch of eggs a female lays down spawning with another dominant male. This behavior is referred to as *Sneaking behavior* (Turner, 1986). Some males can also behave as semi-territorial males, they are darker than females and as soon as dark territorial males are

absent, they occupy their territories for several minutes in an effort to mate with their females (Oliveira and Almada, 1998c). Multiple paternity have been described in cichlids egg bunches (Kellogg et al., 1995).

After the very first hours, the dominance hierarchy of a fish group is already established, formed by dyadic agonistic interactions (Oliveira and Almada, 1998a). Competing males show ritualized behavior of *Visual display* sequences (Leiser et al., 2004) described in several related cichlid species (Baerends and Baerends-Van Roon, 1950; Enquist et al., 1990) to inform rivals about their body size reciprocally (Kelley and Grant, 1993; Oliveira et al., 1998a). Contest can also escalate into physical fight with chasing and biting (Brick, 1998). Although, territorial competitions are mostly ritualized and the winner is determined on the basis of mutual assessment of relative RHP of both rivals (Turner and Huntingford, 1986; Turner, 1994) even so, defeated individuals may suffer higher energy costs than winners (Neat et al., 1998). The dominance hierarchy status is demonstrated through urine chemical signals as well (Oliveira et al., 1996). Dominant males only store urine in their bladders and actively exude it during competitions to transmit dominant odorants - androgens (Miranda et al., 2005; Barata et al., 2008). The amount of excreted androgens provides information about male's RHP (Oliveira and Canario, 2000). Bladder is larger and more muscular in dominant males than in subordinate male (Keller-Costa et al., 2015). Dominant males are generally more successful in territory defense, build larger nests and have bigger mating success (Oliveira et al., 1996; Oliveira and Almada, 1998a; Amorim and Almada, 2003). Higher dominance status is also linked to higher *Gonadosomatic index* (weight of gonads relative to body weight), higher androgen levels, and more vigorous mating behavior (Oliveira and Canario, 2000). During courting and subsequent mating, territorial males produce low-frequency pulse acoustic signals to attract females and to synchronize gamete release during spawning (Amorim et al., 2003b). Territorial males who manage to defend their nest elicit more acoustic signals than defeated males, presumably to provide females with information about mating readiness (Amorim and Almada, 2005). Dominant males exhibit higher levels of androgens and consequently more courting behavior towards females (Oliveira and Canário, 2000). Subordinate males suffer from stress, which leads to increased stress hormones level (Overli et al., 1999), which may than preclude courting behavior (Pankhurst and Van Der Kraak, 2011). Large males are also more successful in defending highly valued territory (Johnsson et al., 1999; Leiser et al., 2004). Even small difference in the size of competing male cichlids determines the outcome of the conflict (Enquist et al., 1990; Draud and Lynch, 2002). Large residents defeat small invaders by often by *Visual displays* only. In an encounter

of small residents with large intruders, contest escalates rapidly and a large number of agonistic interactions occur (Turner, 1994). These results confirm *Prior residency* to be an important competitive factor. Also previous competition experience, *Winner-loser effect* influences contest outcome, mating success and spawning behavior in Mozambique tilapia *O. mossambicus* (Amorim and Almada, 2005).

4.2 EUROPEAN CATFISH

European catfish (*Silurus glanis*, Linnaeus, 1758) influence species structure as it has been described as a dangerous, rapidly spreading invasive species in a number of European regions (Wysujack and Mehner, 2005; Copp et al., 2009). Its production increases in aquaculture, especially in Central and Eastern Europe also in aquaculture. European catfish *S. glanis* is the largest European freshwater fish, which is typical with its rapid growth and adult size and therefore is a highly valued fish trophy (Brzuska and Adamek, 1999). Original areas of occurrence include the tributaries of the Caspian Sea, Black Sea, Aral Sea, Aegean Sea, eastern parts of the Mediterranean Sea, some tributaries of the Baltic Sea and the upper streams of the Rhine (Carol et al., 2007; Alp et al., 2004). By the guilt of the popularity as fish trophy, this species was introduced into many European countries such as France, Italy, Spain, Great Britain or the Netherlands (Elviry, 2001). Recently, concerns about the negative impact of European catfish *S. glanis* on ichthyofauna structure in the regions where it was introduced are growing (Copp et al., 2009). Behavioral ecology of European catfish *S. glanis* in its natural habitat is not fully described, yet, as observation of this large species living on the bottom of large rivers and lakes is difficult (Carol et al., 2007). Most behavioral studies are focused on foraging behavior, growth and aquaculture (Haffray et al., 1998; Alp et al., 2004; Paschos et al., 2004). European catfish *S. glanis* feeds on small fish and invertebrates, exceptionally also on small vertebrates such as small mammals or birds (Adamek et al., 1999). Males grow faster than females and can live up to age of 14 years (Haffray et al., 1998; Doğan Bora and Gül, 2004). Growth rate depends on climate and water temperature. Therefore, European catfish *S. glanis* grows faster in stagnant lakes than in flowing rivers (Alp et al., 2004). This largest European predator fish lives in structured social groups (Boulêtreau et al., 2011). Telemetric studies monitoring the movement of European catfish *S. glanis* in a natural habitat are rare (Carol et al., 2007; Slavík et al., 2007; Slavík and Horký, 2009). Most of the time, European catfish *S. glanis* spend in low streams of large rivers and in muddy bottom lakes, in litoral zone with dense vegetation or near large stones or trunks (Adamek et al., 1999; Alp, 2004). Movement activity generally peaks during night, however

activity varies considerably during seasonal cycles. During high summer season European catfish *S. glanis* is active during the day as well, while in autumn during the night only (Slavík et al., 2007). Night activity peaks are motivated primarily by foraging behavior and searching for prey. This activity is characterized by short movements around a territory (Carol et al., 2007). European catfish *S. glanis* chase their prey led by chemical sense (taste and smell) or by mechanosensory stimuli detected by its lateral line (Pohlmann et al., 2001). Large catfish are highly territorially during the year, especially during mating (Carol et al., 2007) and individuals spend a lot of energy to defend their territories (Alp et al., 2004; Copp et al., 2009). Males reach maturity earlier than females and are ready to mate at the age of three years (less than 80 cm), while females mature at the age of four years (about 90 cm). In the beginning, male digs a pit where female lays down eggs formed into rows. Clutch is fertilized and watched by male until hatch (Alp et al., 2004).

European catfish *S. glanis* is a catch of high value among sport fishermen (Linhart et al., 2004) and it was bred extensively for centuries in some European countries (Linhart et al., 2002; Paschos et al., 2004). Aquaculture production of European catfish *S. glanis* is continuously increasing (Boujard, 1995; David, 2006; Adamek et al., 2015); its production has grown in the Central and Eastern Europe more than three times over ten years (Linhart et al., 2002) and makes annually around 2000 tones (Copp et al., 2009). Since European catfish *S. glanis* is a large territorial species, the aquaculture is always associated with stress. Social hierarchy is well developed and individuals are able to make group decisions based on individual recognition of familiar individuals (Slavík et al., 2012). Behavioral studies of European catfish *S. glanis* are rare, more of behavioral studies were conducted in closely related African catfish *Clarias gariepinus* (Burchell, 1822; Kaiser et al., 1995; Martins et al., 2005). In aquaculture, large individuals are considered dominant and smaller submissive (Brzeski and Doyle, 1995; Chellappa et al., 1999). *Grading* comprise redistribution of fish into groups of same body size (Conte, 2004). Fish sorting leads to increased aggression and stress in fish groups (Martins et al., 2006; Slavík et al., 2011). In this artificially created homogeneous group, individuals have to spend a considerable amount of energy to restore the social hierarchy (Stefánsson et al., 2000) and to compete about resources (Baardvik and Jobling, 1990). Instead of increased growth of small fish, removal of large fish destroys dominance hierarchy and increases aggressive level (Martins et al., 2005). Familiarity plays an important role in resource distribution among individuals (Slavík and Horký, 2009; Slavík et al., 2015). Competitive behavior may also be related to coloring, where pale shades are generally associated with high levels of aggressiveness and dominance (darkening of the body

alleviates the aggression of other individuals) in salmon *S. salar* (Linnaeus, 1758, O'Connor et al. 2000) and Mozambique tilapia *O. mossambicus*, Linnaeus, 1758, (Oliveira and Almada, 1998a). In Oscar fish *Astronotus ocellatus* (Agassiz, 1831) and Nile tilapia *O. niloticus* (Linnaeus, 1758), dark coloration is the sign of dominance (Beeching, 1995; Volpato et al., 2003). In European catfish *S. glanis*, albino individuals were found in aquaculture and natural habitat (Dingerkus et al., 1991).

5 AIMS AND OBJECTIVES

The aim of this thesis is to explore communication channels and their roles in competitive behavior in fish.

- We aimed to develop an experimental procedure to test multimodal communication in competition studies in Mozambique tilapia *O. mossambicus*.
- We aimed to examine the effects of social and environmental factors and individual characteristics on competitive abilities in European catfish *S. glanis*.
- We aimed to examine social and competitive behavior in groups of albino and pigmented European catfish *S. glanis*.

We have developed following testable hypotheses based on literature review:

- Mozambique tilapia *O. mossambicus* is reactive to visual computer manipulated stimuli (computer animation, video record).
- Mozambique tilapia *O. mossambicus* is more reactive to visual stimuli when presented together with acoustical playbacks.
- Body size, resource availability and familiarity decrease activity in European catfish *S. glanis* whereas *Residency effect* increases.
- Level of aggression is higher in albino than pigmented European catfish *S. glanis*.



Computer-manipulated stimuli as a research tool in Mozambique tilapia *Oreochromis mossambicus*

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Abstract Multimodal communication is essential in social interactions in cichlid fish, including conspecifics' recognition, agonistic interactions and courtship behaviour. Computer-manipulated image stimuli and sound playback offer powerful tools to assess the relative relevance of visual and acoustic stimuli in fish behavioural studies, but these techniques require validation for each taxon. The aim of the present study was to investigate whether Mozambique tilapia *Oreochromis mossambicus* responds to computer-manipulated visual stimuli and acoustic playback. Six experiments were conducted: computer animation playback, video playback, interaction with a mirror, presentation of a live male in a jar alone and combined with courting sound playback or with white noise playback. Individual agonistic interactions (lateral displays, up and down swimming, butting) and courting behaviours (tilting leading, digging) were tallied for each experiment. Our results suggest that non-interactive computer-manipulated visual stimuli is not a suitable tool in behavioural research with Mozambique tilapia. In contrast, interaction with a live male in a jar seems to remain the best visual research instrument inducing significant strong behavioural responses. Although none or only a few agonistic

interactions were observed towards video playbacks or computer animations, such interactions significantly increased towards a male in jar and were modulated by courtship sound playback, suggesting the additional relevance of sound playback as a tool in behavioural research with Mozambique tilapia, including the study of multimodal signalling.

Keywords Playback experiments · Visual stimuli · Acoustic signals · Agonistic interactions · Courtship behaviour

Introduction

Communication is a complex process involving different sensory channels, and it is the combination of the different sensory modalities that determines the signal's function and efficacy in many species (Bradbury and Vehrencamp 2011; Smith and Evans 2013), including fish (Hankison and Morris 2003; Maruska et al. 2012). African cichlid use multimodal signals (visual, acoustic, olfactory etc.) to coordinate social behaviour (Van Staaden and Smith 2011). Presence of all relevant cues is crucial for eliciting appropriate behavioural response (Ripley and Lobel 2004). Particular elements of the signal can be highly important, as they might have evolved together (Ghazanfar and Schroeder 2006). Assessing the relative role of different components of multimodal signals or of different signal parameters within a sensory channel is essential to better understand communication and social interactions (Candolin 2003). 'Cue-Isolation Experiments', the most common approach to investigate the function and efficacy of multimodal signals, present a receiver with each signal separately first and then compare these responses to the ones elicited by combined multimodal signal (Smith and Evans 2013).

Experiments exploring computer-manipulated visual stimuli are considered to be a relatively cheap and simple tool for

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preference studies in fish (Baldauf et al. 2009). Image computer processing allows to manipulate single traits of visual signals (body size and shape, coloration and colour patterns) or combine them while keeping constant other variables (Wong and Rosenthal 2006; Butkowski et al. 2011). Moreover, by modifying specific features independently, the effects on the behavioural response can be successively determined, and the signal function of those features can be reliably detected (Rowland 1995; Künzler and Bakker 2001; Kodric-Brown et al. 2006). When testing for the importance of acoustic signals in animal behavioural interactions, playback tests are a major tool because they also allow control over experimental conditions (Bertucci et al. 2013). Nevertheless, sound playback experiments in fish are rare, probably due to limitations of underwater loudspeakers, which do not reproduce fish sounds appropriately (Fonseca and Maia Alves 2012). In addition, co-occurrence of visual stimuli appears to be indispensable to evoke adequate behavioural response in several fish species (Ripley and Lobel 2004; Smith and van Staaden 2009; Amorim et al. 2013). Consequently, developing bioassays where both sensory channels can be manipulated, which are lacking in fish literature, would be of major advantage to test the function of multimodal signals in this taxon (Baldauf et al. 2010; Amorim et al. 2013). The aim of this study was to develop an experimental procedure to test multimodal communication in a cichlid fish by investigating whether animals respond to computer-manipulated visual stimuli and acoustic playbacks.

Cichlids are excellent models to test multimodal communication in fish since they are key laboratory models (e.g., Maruska et al. 2012) and intra-species communication is based on multimodal stimuli (Escobar-Camacho and Carleton 2015), including visual (Baldauf et al. 2010; Dijkstra et al. 2010) and acoustic signals (Ladich and Schultz-Mirbach 2013; Maruska et al. 2012; Estramil et al. 2013). For example, visual communication is essential in species recognition (Seehausen et al. 2008), agonistic interactions (Oliveira and Almada 1998a) and courtship behaviour (Amorim et al. 2003). Likewise, acoustic signals play an important role in mate choice (Simões et al. 2008; Verzijden et al. 2010) and aggressive interactions (Bertucci et al. 2010; Longrie et al. 2013).

Six experiments comprising different visual and acoustic stimuli sets, including computer animation playback, video playback, interaction with a mirror, presentation of a live male in a jar alone and combined with courting sound playback or white noise playback, were conducted with the Mozambique tilapia *Oreochromis mossambicus* (Peters 1852), a maternal mouth-brooding cichlid that relies on multimodal signals during social interactions (Amorim et al. 2003; Keller-Costa et al. 2015). Different types of agonistic (lateral displays, up and down swimming, butting) and courting behaviours (tilting, leading, digging) were analysed to evaluate whether computer-manipulated stimuli was a relevant tool to be used with Mozambique tilapia. Considering results of previous

studies (Amorim et al. 2003; Oliveira et al. 2005; Baldauf et al. 2009), we predicted that Mozambique tilapia would exhibit different agonistic and courting behavioural components towards the presented visual and acoustic stimuli.

Material and methods

Study fish

Mozambique tilapia *O. mossambicus* (Peters, 1852) is a maternal mouth-brooding cichlid lek-breeding in African lakes and rivers (Bruton and Bolt 1975). Females attracted to a territorial male spawn in its nest pit and, after fertilization, recover the eggs in her mouth and abandon the locality (Oliveira and Almada 1996a). When fighting for a territory and establishing social hierarchies, males engage in frequent male-male agonistic interactions where they use both visual and chemical signals (Keller-Costa et al. 2015). Besides visual and chemical displays (Keller-Costa et al. 2015), territorial males also produce low-frequency pulsed acoustic signals (drums) during courtship and spawning (Amorim et al. 2003; Amorim and Almada 2005).

Mozambique tilapia used in the present study were descended from stock kept at Aquário Vasco de Gama (Lisbon, Portugal) since the 1970s, originally caught in the Incomati River, Mozambique. A total of 52 fish were kept in mixed sex groups (around 20 sex mature individuals, 2–3 territorial males) in 200-L stock aerated aquaria under 12L/12D photoperiod. Water temperature was kept at 26 ± 0.5 °C. Fish were fed once a day with tropical fish flakes. In total, 30 fish, five individuals for each of the six experiments were tested.

All experimental and animal care procedures comply with animal welfare laws, guidelines and policies, and all efforts were made to maximize animal welfare. There were intensive aggressive interactions neither towards females nor towards males, as males were in separate tanks during experiments. All subject fish survived and were used in subsequent laboratory experiments. All fish exhibited normal behaviour within few minutes of being returned to stock tanks, suggesting that they were not exposed to abnormal stressful situations.

Experimental setup

The experimental tank (90 × 40 × 40 cm, ≈145 L) had a layer of fine gravel with a pit in the middle that was used as a nest by the subject male during courtship interactions. The sides of the tank were lined with opaque grey partitions at both ends and removable cardboard on the laterals to reduce visual disturbance from the laboratory environment. The tank rested on a concrete slab (10 cm thick) supported by a 50-cm Rockwool layer that effectively uncoupled the tank from floor transmitted vibrations. A fluorescent tube (40 W) 70 cm above

illuminated the tank. Visual stimuli (a computer monitor with animation or video playback, a mirror, or a male in a jar, see below) were placed opposed to one end of the tank (Fig. 1a, b). A computer monitor (Samsung SyncMaster 172V, LCD/TFT active matrix monitor, 1280 × 1024 resolution, 32 bit colour depth, 75 Hz refresh rate) was used to playback the video or animation. On the opposite side, an underwater camera (MVC2000-WP-LED, Micro Video Products, Bobcaygeon, Ontario, Canada) was attached 20 cm above the bottom to the PVC grey partition (5 mm thick) to record the fish behaviour (Fig. 1a, b) through a Terratec Grabby (Nettetal, Germany) frame grabber controlled by Maggix to a laptop. From this position, the camera allowed to record fish responses to the image on the screen, the mirror, or the stimulus fish (see below).

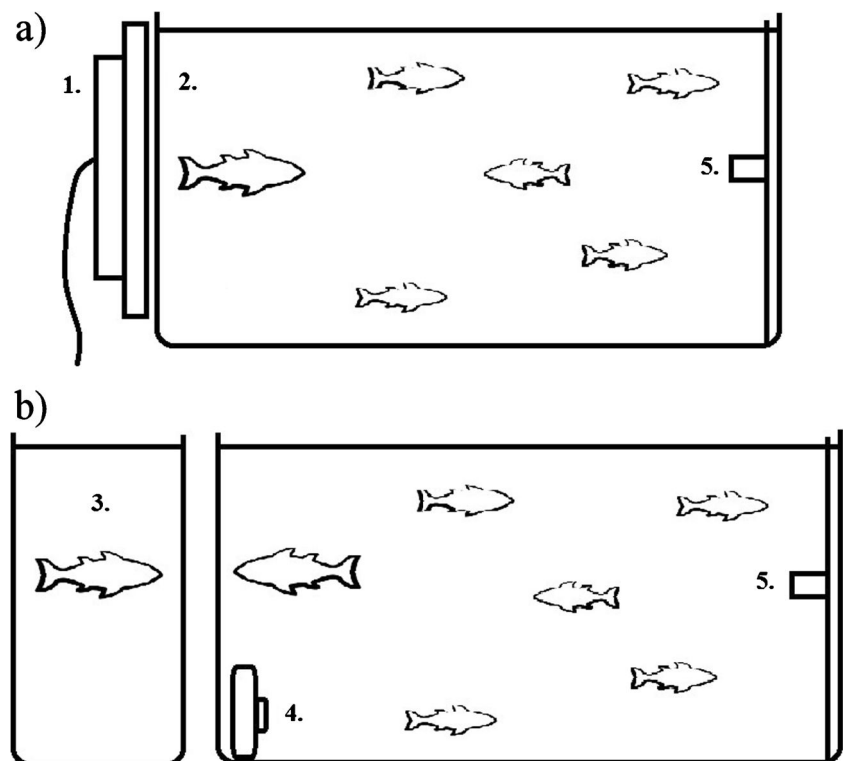
Sound playbacks were performed using a custom-made device composed by an underwater speaker and a driver (Fonseca and Maia Alves 2012) placed in the middle of the tank wall, where the visual stimuli were also presented (Fig. 1b). The sound playback device is able to reproduce low-frequency pulsed fish sounds with great accuracy (Fonseca and Maia Alves 2012). Sounds were fed through a D/A converter (Edirol UA-25, Roland, Japan; 16 bit, 8 kHz) controlled by Adobe Audition 3.0 (Adobe Systems Inc., Mountain View, CA, USA). The amplitude of the courtship sound playback was calibrated with a hydrophone (Bruel and Kjaer 8104, Bruel and Kjaer, Naerum, Denmark, sensitivity -205 dB re1V/1 Pa; frequency response within 1 dB from

0.1 Hz to 180 kHz), connected to a sound level meter (Bruel and Kjaer 2238 Mediator, Naerum, Denmark) and adjusted to mimic the amplitude of tilapia male sounds at 3.0–4.5 cm distance measured in previous experiments (MCP Amorim and PJ Fonseca unpublished data). White noise playback was adjusted to present similar RMS amplitude. Image or sound playbacks were used according to the specific experiment (see below).

Pre-test of males' motivation

A preliminary test was used to verify the motivation of subject males to court females and defend territories. A black coloured territorial male exhibiting agonistic behaviours in the stock aquarium (lateral display, nest defence, fights and bites) was transferred to the experimental tank. During the next hour, the computer screen showed the grey background (R G B: 238, 238, 238) to habituate the fish to the background used in playback trials. After this period, five sexually mature females were introduced into the tank by removing the partition, to induce courting behaviour by the subject male usually accompanied by pigmentation darkening typical of territorial males. Then, a 15-min acclimatization period was allowed followed by 20-min video recording. Interactions between the subject male and the females were used to assess the spawning readiness of the male. The behaviour was categorized according to Oliveira and Almada (1998b), and the occurrences of tilting, leading, nest digging, lateral displaying

Fig. 1 a, b Experimental setup depicting the position of the stimulus. 1 Computer screen (Exp. 1, 2), 2 mirror (Exp. 3), 3 male in a jar (Exp. 4, 5, 6), 4 underwater speaker (Exp. 5, 6), 5 underwater camera (Exp. 1, 2, 3, 4, 5, 6)



and butting were counted. We also created a new category of 'up and down swimming', where fish swims up and down in close proximity to the stimulus. This is a typical behaviour observed in aquaria in this and other cichlids (personal observation) in response to a stimulus that they cannot interact directly with. Following Oliveira and Almada (1998b), we assessed three body colour levels: dark 1, dark 2 and dark 3, associated to increasing courting interest and spawning readiness of the subject male. Dark 1 characterized by a neutral silver body, beginning to darken above the pelvic region. Dark 2 recognized as body darkening with scattered darker areas on the belly and on the caudal fin and the sub-opercular region light. Dark 3 assigned to a black body, white lower jaw and opercula, a white rim in the dorsal, anal and caudal fins and reddish pelvic fins. Males with no courting behaviour and pale colour pattern (Dark1) were excluded from the subsequent experimental trial. The ratio of receptive to non-receptive males was approximately 1.5/1. Receptive and non-receptive males did not differ in weight or standard length.

Experiments

Thirty territorial males (standard length, SL, mean \pm SD: 8.33 ± 0.39 cm; total length, TL: 10.55 ± 1.09 cm; and weight, W: 18.39 ± 5.39 g) were used to test fish reactions to six different visual and acoustic stimuli sets. Those consisted of a computer two-dimensional (2D) animation (Exp. 1), a video playback (Exp. 2), a mirror image (Exp. 3), a male in a jar (a territorial black coloured male in a small glass container $15 \times 15 \times 30$ cm, Exp. 4), a male in a jar combined with playback courting sounds (Exp. 5) or combined with white noise (Exp. 6). Five males were tested in each of the six experiments, chosen randomly out of the 30 territorial males. After every trial, the experimental male was allocated to a different tank so it was not used repeatedly. Each male was exposed to one treatment only. Each trial lasted for 15 min, conducted in late morning (10–12 am). Different treatments (experimental trials) were carried out in a varied order, one treatment per day. Females were reused after a period of at least 4 weeks in stock tanks. Neither males nor females were fed during the pre-test stimulation or during the experiments. Videos were analysed with Etholog (v2.2, Ottoni 2000) (<http://www.ip.usp.br/docentes/eottoni/EthoLog/ethohome.html>). The number of agonistic behaviours (butting, lateral display, up and down swimming) and courting behaviours (tilting, leading, nest digging) was tallied. We used the total number of agonistic behaviours as the main behaviour response indicator.

Exp. 1 Computer animation: RAW digital images were taken from three sexually mature territorial black coloured males ca. 10 cm long (TL) to maintain a 1:1 ratio between animated image and focal males (ca. 10 cm TL). The digital images were dissected from the background with Adobe Photoshop 4. Animations of dissected male images were prepared using

the 'animation paths' tool of PowerPoint 2008 over a grey (RGB: 238, 238, 238) background with a resolution of 1024×768 pixels. In our animations, fish were mainly kept in diagonal and lateral positions to emphasize lateral displaying from a territorial male. The stimulus image started at the top right corner of the screen and moved to the middle bottom, where it was hovering with wide spread dorsal, pelvic and caudal fins characteristic of agonistic displays in this species. The sequence continued with simulation of digging in a pit, followed by hovering over the pit and a lateral display. Finally, it moved towards the top left corner where it turned around and repeated the same path in the opposite direction. Digging was included since it is a territorial behaviour that increases in frequency in the presence of conspecific males as it advertises territorial ownership (Oliveira and Almada 1998a; Amorim et al. 2003).

Exp. 2 Video playback: Two 3-min videos of black coloured (Dark 3) territorial males mouth fighting over a pit were played back to each of five territorial males assessed as receptive individuals. The 3-min video recordings were looped 5 times in a total of 15 min. The video playback had to be adjusted so that the size ratio between the video male and the focal males was maintained to approximately 1:1 as above. This stimulus was chosen as watching conspecific agonistic interactions is known to prime aggressive motivation of spectators (bystander effect) in this species (Oliveira et al. 2001).

Exp. 3 Mirror image: A mirror (20×40 cm) replaced the video playbacks, and agonistic interactions towards the own image (Elwood et al. 2014) were recorded.

Exp. 4 Male in a jar: A male in a jar was placed in the experimental tank at the video/mirror stimulation side. The jar with the stimulus male was allowed 20-min acclimatization, separated by a grey partition from the remaining experimental tank. The subject and stimulus fishes were size-matched. Note that in this setup (as in Exp. 5 and 6), subject males were not exposed to sounds made by the male in the jar as this species only makes sounds during courtship interactions (Amorim et al. 2003).

Exp. 5 Male in a jar + courting sounds: The underwater speaker was placed next to the male in jar, in lateral position and facing the middle of the experimental tank. Courtship sounds were played back to the subject male during the interactions with the stimulus male. The playback sounds were selected from a data set of previously recorded *O. mossambicus* courtship sounds. We selected sounds from 4 different males (standard length, SL, mean \pm SD: 11.05 ± 0.82 cm; total length, TL: 14.13 ± 0.76 cm; and weight, W: 37.75 ± 5.39 g) that showed high courting motivation in previous experiments. Each 1-min

sound file was looped and included 5 sounds from one male with intervals falling within natural variation of motivated fish.

Exp. 6 Male in a jar + white noise: The experiment was similar to the previous one, but the courtship sound was replaced with white noise. A white noise stimulus playback was prepared with sequences of 10 s, 2 kHz low pass filtered white noise followed by 2 s pauses, regularly repeated.

Mozambique tilapia behavioural categories

We used the ethogram described for Mozambique tilapia by Oliveira and Almada (1998b) and considered the agonistic categories ‘lateral display’ and ‘bulling’ towards another male. As no interaction between the focal male and visual stimulus is possible, focal male usually ram with open mouth in glass side of an experimental tank or a mirror. We additionally defined ‘up and down swimming’ characterized by a territorial male moving up and down together with the opponent or its image. Territorial males might also exhibit courting behaviour such as tilting, leading or nest digging (Oliveira and Almada 1998b).

Statistical analysis

Statistical analyses were performed with SAS (version 9.2; SAS Institute Inc., Cary, USA). Total number of agonistic behaviours and the number of specific agonistic and courting behaviours were analysed using separate mixed models with random factors (PROC GLIMMIX with Poisson distribution). Random factors were used to account for a subject effect. The significance of each exploratory variable (i.e. fixed effect treatment, TL, SL, W, including their interactions) in the particular model was assessed using an F test in which we sequentially dropped the last significant effect, beginning with the full model (backward selection procedure). Least square means (LSM), henceforth referred to as ‘adjusted means’, were computed for treatment levels (i.e. experiment type). Post hoc pairwise comparisons were tested with a t test and a Tukey–Kramer adjustment. The degrees of freedom were calculated using the Kenward–Roger method (Kenward and Roger 1997).

Results

During the pre-test procedure, the total number of interactions ($F_{2,30} = 9.71$, $P < 0.0006$; Fig. 2a, Table 1) and the number of tilting ($F_{2,30} = 11.84$, $P < 0.0002$; Fig. 2b, Table 1) and nest digging ($F_{2,30} = 4.75$, $P < 0.0162$; Fig. 2c, Table 1) increased with darkening of the experimental fish. These results validate the responsiveness assessment of males in the pre-test procedure, showing that the colour pattern of tilapia males, associated with

territoriality and dominance, is a good indicator of intraspecific behavioural reactivity, including courting readiness. No relationship between the size (TL, SL, W) of the subject male and the number of courting or agonistic behaviours was found.

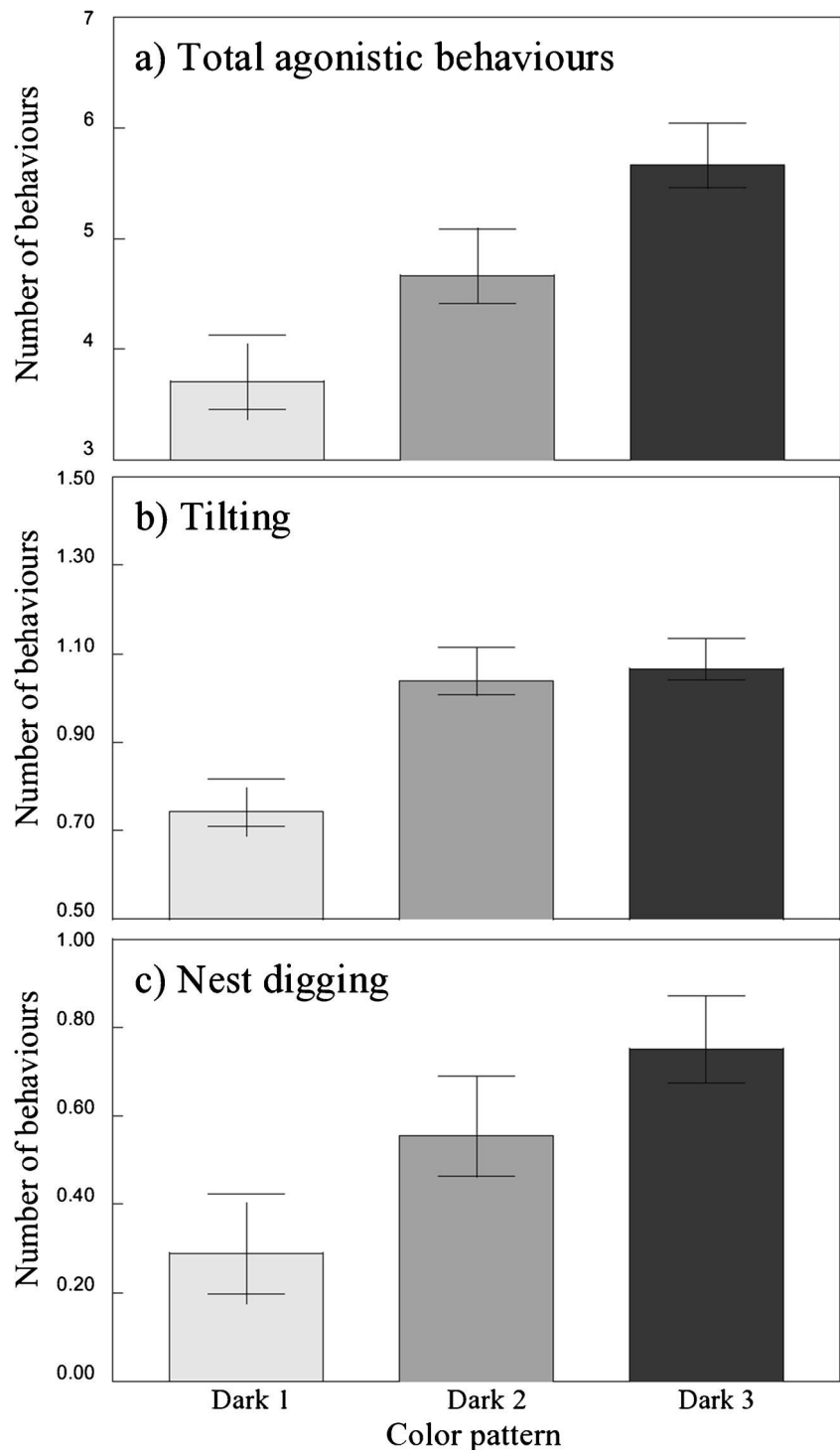
Experiments revealed that the total number of agonistic behaviour ($F_{5,30} = 5.52$, $P < 0.001$; Fig. 3a) was highest when the tested male interacted with the mirror (Exp. 3), or with a male in a jar (Exp. 4), either alone or when combined with courting sound (Exp. 5) or white noise (Exp. 6). No difference was found among these treatments ($P > 0.05$). Although a lower number of total agonistic interactions was observed under non-interactive computer animation (Exp. 1) and video playback (Exp. 2) stimuli, these did not differ significantly from mirror and white noise treatment (Fig. 3a, Table 2).

Differences among treatments for single agonistic behaviours (butting, $F_{5,30} = 6.96$, $P < 0.0002$, Fig. 3b; lateral display, $F_{5,30} = 5.34$, $P < 0.0013$, Fig. 3c; up and down swimming, $F_{5,30} = 7.08$, $P < 0.0002$, Fig. 3d, Table 2) followed similar overall patterns. The lowest numbers of interactions were also induced by computer animation and video playback in each category of agonistic behaviour, suggesting a generally weak response to these artificial visual stimuli. Our results point to an increased intensity of lateral displays and up and down swimming exhibited by subject males towards a male in a jar combined with courting sound. In contrast, butting was mostly evoked by the presence of a male in a jar, not only showing that visual contact with another interacting male is sufficient to trigger this escalated agonistic behaviour, but also that its combination with conspecific sound significantly decreases the aggression level. In contrast to courtship sounds, the effect of white noise did not enhance lower intensity agonistic behaviour (lateral display and up and down swimming) (cf. Fig. 3c, d, Table 2), but was not different from courtship sound playback in its effect reducing escalated agonistic butting (Fig. 3b, Table 2). No relationship between the size (TL, SL, W) of the subject male and the number of agonistic behaviours was found.

Discussion

This work aimed to test the relevance of using computer image animations, video playbacks and sound playbacks as tools in behavioural studies with Mozambique tilapia *O. mossambicus* and was based on experiments with other fish species (stickleback *Gasterosteus aculeatus*, Bakker and Künzler 1998; cichlid *Pelvicachromis taeniatus*, Baldauf et al. 2009). A number of behavioural experiments using computer-manipulated visual stimuli were previously conducted to investigate anti-predator behaviour (Evans et al. 1993; Rosenthal 2000), male aggression (Turnell et al. 2003; Saverino and Gerlai 2008) and mating preferences (Künzler and Bakker 2001; Thunken et al.

Fig. 2 Number (adjusted means \pm SE) of total agonistic behaviours (a), tilting (b) and nest digging (c) behaviours across three different colour patterns in territorial males



2011). Although computer-manipulated visual stimuli have been repeatedly used for behavioural research in different fish species, namely in cichlids (Balshine-Earn and Lotem 1998; Baldauf et al. 2009; Thunken et al. 2011; Thunken et al. 2014), our study revealed weak behavioural responses to non-interactive computer-manipulated visual stimuli (animation and video playbacks) by

dominant males of the Mozambique tilapia, despite their responsiveness to other stimuli.

There are a number of limitations to the use of computer-manipulated stimuli in behavioural experiments. For example, using computer image animations, video or sound playbacks in an attempt to control a single stimulus may limit its effectiveness as multiple signals may be requested to elicit an

Table 1 Pairwise comparisons of pre-test procedure analysis

Dependent variable	Figure	Independent variable	Pairwise	Adj. <i>P</i> <
<i>Total agonistic behaviours</i>	2a	Colour	1 × 2	0.1266
			1 × 3	0.0004
			2 × 3	0.0809
<i>Tilting</i>	2b	Colour	1 × 2	0.0014
			1 × 3	0.0002
			2 × 3	0.9216
<i>Nest digging</i>	2c	Colour	1 × 2	0.2391
			1 × 3	0.0119
			2 × 3	0.3998

References to related figures and *P* values resulting from the Tukey–Kramer adjustment are included

adequate behavioural response since multimodal communication is widespread in nature (Candolin 2003; van Staaden and Smith 2011; Veen et al. 2013; Yong et al. 2013). Playbacks of manipulated visual stimuli using R(ed) G(reen) B(lue) video screens, which were developed according to human sight, may represent a serious constraint for the visual perception by other animals with visual pigments exhibiting different absorption spectra (Rosenthal 2007) and different time constants of the visual pathway (effect of video screen frame rate, Rowland 1999; Baldauf et al. 2009). Another constraint may

rely on the lack of three-dimensional depth cues of video monitors (Zeil 2000; Stevens et al. 2007), which contrasts with natural visual stimuli. Furthermore, the spectral composition of the light (e.g. presence of ultraviolet components) (Rosenthal 2000; Baldauf et al. 2009) and the absence of light polarization (Hawryshyn 2010; Hornsby et al. 2013; Chen et al. 2015) may affect the way stimuli are perceived. Likewise, natural motion patterns (Clark and Stephenson 1999), speed and velocity (Woo and Rieucau 2011) may also play a role in the perception of the stimuli by the fish and

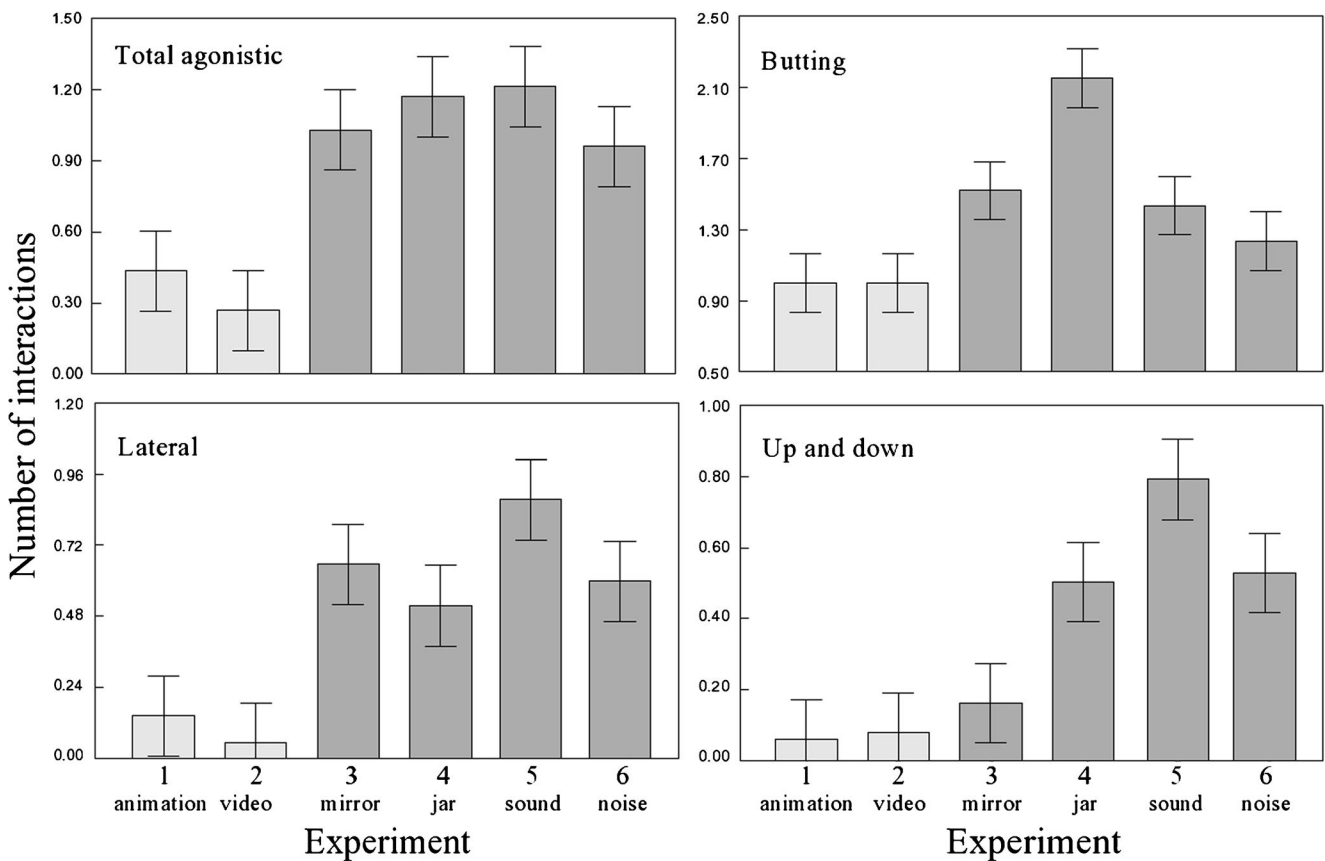


Fig. 3 Number (adjusted means ± SE) of total agonistic behaviours (a), butting (b), lateral display (c) and up and down swimming (d) across six experiments

Table 2 Pairwise comparisons of experimental analysis

Dependent variable	Figure	Independent variable	Pairwise	Adj. $P <$
<i>Total agonistic behaviours</i>	3a	Treatment	animation × jar	0.0463
			animation × mirror	0.1603
			animation × noise	0.2678
			animation × sound	0.0305
			animation × video	0.9808
			jar × mirror	0.9910
			jar × noise	0.9494
			jar × sound	1.0000
			jar × video	0.0085
			mirror × noise	0.9997
			mirror × sound	0.9708
			mirror × video	0.036 L
			noise × sound	0.8948
			noise × video	0.0691
sound × video	0.0053			
<i>Butting</i>	3b	Treatment	animation × jar	0.0003
			animation × mirror	0.2445
			animation × noise	0.9095
			animation × sound	0.4321
			animation × video	1.0000
			jar × mirror	0.0976
			jar × noise	0.0050
			jar × sound	0.0432
			jar × video	0.0003
			mirror × noise	0.8144
			mirror × sound	0.9990
			mirror × video	0.2445
			noise × sound	0.9513
			noise × video	0.9095
sound × video	0.432 L			
<i>Lateral display</i>	3c	Treatment	animation × jar	0.4075
			animation × mirror	0.1152
			animation × noise	0.2044
			animation × sound	0.0083
			animation × video	0.9966
			jar × mirror	0.9767
			jar × noise	0.9979
			jar × sound	0.4472
			jar × video	0.1878
			mirror × noise	0.9996
			mirror × sound	0.8663
			mirror × video	0.0407
			noise × sound	0.7115
			noise × video	0.0794
sound × video	0.0024			
<i>Up and down swimming</i>	3d	Treatment	animation × jar	0.0836
			animation × mirror	0.9859
			animation × noise	0.0586
			animation × sound	0.0009
			animation × video	L.0000
			jar × mirror	0.2870
			jar × noise	1.0000
			jar × sound	0.4703
			jar × video	0.1090
			mirror × noise	0.2177
			mirror × sound	0.0050
			mirror × video	0.9948
			noise × sound	0.5706
			noise × video	0.0775
sound × video	0.0012			

References to related figures and P values resulting from the Tukey–Kramer adjustment are included

should be considered while using computer-manipulated stimuli. Therefore, the weak behavioural response of tilapia males to our played back videos and image animations might be related to technical limitations not obvious to a human observer and to inadequacies of the motion patterns. In addition, in contrast with live and mirror treatments, both the animation and video stimuli were not interactive which may have hindered an agonistic response from focal males suggesting that interactive computer-manipulated stimuli still need to be tested to ascertain whether these tools are not appropriate for behavioural research in this species. For example, in another African cichlid species, *Astatotilapia burtoni*, video playback did not elicit behavioural response of the same strength as live interacting fish (Chen and Fernald 2011). Although all visual stimuli were designed to elicit an agonistic response (Saverino and Gerlai 2008; Baldauf et al. 2009), live and mirror stimuli were interactive, while computer animation and video playback stimuli were not, likely impairing assessment between opponents. This distinction between experimental treatments may cause different type of agonistic response between treatments (D'Eath 1998; Zeil 2000).

The use of a mirror allows to simulate competitive situations eliciting agonistic behaviours while preventing the subject fish from being hurt during a real fight (Balzarini et al. 2014). However, a mirror image may not evoke the same behavioural responses as a living conspecific, as displays towards a real opponent are more frequent than when facing a mirror image (Elwood et al. 2014). Our experiments led to similar results, as agonistic interactions, except for the lateral displays, were more frequent towards a male in a jar than against the mirror reflection.

Acoustic signals play an important role in intraspecific communication of many fish species, including Mozambique tilapia and other cichlids (Amorim et al. 2003; Verzijden et al. 2010) and should therefore be considered for playback experiments in addition to visual stimuli (Ripley and Lobel 2004; Smith and van Staaden 2009) or other communication signals. Sound playback experiments in fish, however, remain rare likely due to technical limitations of underwater loudspeakers that often do not allow to appropriately reproduce fish sounds (Ladich 2004; Fonseca and Maia Alves 2012). In most behavioural experiments, no response to sound playbacks was found when these were not accompanied by visual stimuli (Lugli et al. 1997; Maruska et al. 2012; Amorim et al. 2013). In our experiments, courtship sound combined with a live male in jar provoked a similar behavioural response (total agonistic behaviour) than a live male in jar alone or combined with white noise. Interestingly, the frequency of escalated agonistic behaviour (butting) was reduced, while lower intensity agonistic behaviour (lateral displays) and up and down swimming was apparently enhanced by the simultaneous exposure to courtship sounds. Such results are in accordance with the work of Schwarz (1974) and Bertucci et al. (2010) that showed a reduction in aggressiveness by cichlid males engaged

in agonistic interactions when visual contact was accompanied by playbacks of agonistic sounds. Since the repertoire of Mozambique tilapia does not appear to include agonistic sounds (Amorim et al. 2003), it is remarkable to observe a similar effect induced by courtship sounds in this species. Surprisingly, the reduction in butting behaviour was similar regardless of sound type (conspecific vs white noise). White noise may act as a disturbance factor and may therefore lower natural behavioural response to a rival male. The disturbance effect of noise disrupting natural behavioural responses is well known in fish (Ladich and Schultz-Mirbach 2013).

We can conclude that the use of a live male in a jar and sound playback of conspecific sounds appear to be relevant tools for behavioural studies with Mozambique tilapia. In contrast, computer-animated video images and video playbacks using RGB computer screens did not elicit significant agonistic reactions by males. Nonetheless, further research using interactive stimuli is required. As communication in this and other fish species utilizes multimodal sensory cues, using a combination of different artificial visual stimuli with other sensory modalities is worthwhile to disentangling sensory integration and multimodal communication in fish.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study.

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Familiarity, prior residency, resource availability and body mass as predictors of the movement activity of the European catfish

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Abstract When animals compete for resources, their competitive abilities and behavioural strategies can be expressed as changes in movement activity. Stress is an important predictor of activity, and the variability of this predictor reflects the impact of environmental and social factors, while the effects of stress are further influenced through individual behavioural syndromes. We examined the effects of social (familiar vs. unfamiliar and resident vs. intruder) and environmental (resource availability) factors and individual characteristics (body mass) on the movement activity of juvenile European catfish *Silurus glanis* (L.). Familiarity and prior residency decreased the movement activity of these catfish, whereas resource unavailability significantly increased the movement activity of intruders to a level 1.5 times greater than that of the residents. The occurrence of an interaction involving an individual whose body mass was higher than that of individuals from the opposite group predicted a low level of movement activity of this individual. These results suggest that familiarity, prior residency, and high body mass decrease stress from the limited availability of resources.

Keywords Movement activity · Prior residency · Familiarity · Body mass · Shelter · *Silurus glanis*

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Introduction

When animals compete for resources, their competitive abilities and behavioural strategies can be expressed as changes in movement activity. This activity has been positively correlated with higher growth rate, larger size and shorter development (Werner and Anholt 1993), as more active animals frequently encounter more food (Olsson et al. 2002; Brodin 2008; Liebgold and Dibble 2011). The levels of activity can be explained as predictable animal behaviour in response to changes in the environmental conditions (MacArthur and Pianka 1966) and/or expression of individual personality consistent with time and across conditions (Sih et al. 2003, 2004; Brodin 2008; Conrad et al. 2011).

The relationship between the activity of animals and environmental conditions shows that level of activity correlates with geographical (Liebgold and Dibble 2011), seasonal (Valdimarsson et al. 1997; Benito et al. 2015) and diurnal variability (Alanära et al. 2001; Brännäs 2008). The activity of animals is further influenced through mutual interactions, and the level of activity reflects the social status of an individual (Gómez-Laplaza and Morgan 2003). Large and dominant individuals are active at times suitable for food intake and when predation risk is low, whilst subdominant individuals are diurnally active (Metcalfe et al. 1999; David et al. 2007) and have larger home ranges (Nakano 1995). Groups containing familiar individuals are more active and better at resource exploitation and predation avoidance compared with unfamiliar conspecifics (Höjesjö et al. 1998; Griffiths et al. 2004; Liebgold and Dibble 2011). Territory holders compete for the territory more actively with intruders than neighbours (Booksmythe et al. 2010), and active individuals more effectively defend the territory than less active conspecifics (Sikkel and Kramer 2005).

Consistent individual differences in activity have been observed for individuals in ecological situations in which the behavioural syndromes are measured (Réale et al. 2007; Conrad et al. 2011; Sih et al. 2012), e.g. in brook charr *Salvelinus fontinalis* (M.), suggesting two alternative feeding strategies based on high activity and consistent behaviour and/or low activity and plastic behaviour (McLaughlin et al. 1992; Wilson and McLaughlin 2007; Farwel and McLaughlin 2009). Activity is often a substitutive demonstration of an individual status, e.g. stress. Øverli et al. (2005) described the consistent behavioural traits of individuals in a group of rainbow trout *Oncorhynchus mykiss* (W.) selected for low and high cortisol response to stress, showing faster acclimatisation to novel environments and decreasing activity in the presence of intruders with low cortisol responses. Animals show decreased activity in the stressful presence of familiar predators (Brodin and Johansson 2004; Brodin et al. 2006) and/or dominant conspecifics (Rudolf 2007). Furthermore, different levels of activity accompanied with stress can be expected for residents and intruders, reflecting differences in motivation that can be won and/or lost (Wolf et al. 2007); intruders are expected to be more active, as these individuals are bolder, more exploratory and/or aggressive (Cote et al. 2010, 2015).

The aim of the present study was to analyse the movement activity in European catfish *Silurus glanis* (L.) as a response to multiple stressful factors. Europe's largest freshwater predator (Copp et al. 2009) lives in groups (Boulétreau et al. 2011), shows variability in movement activity across seasons and diurnal rhythms (Slavík et al. 2007), and displays individual differences in energy consumption (Slavík and Horký 2012) which are higher when fish are exposed to stressful contact with unfamiliar individuals (Slavík et al. 2011).

We examined the effects of individual characteristics (body mass), and social (familiar vs. unfamiliar, resident vs. intruder) and environmental factors (resource availability) on the movement activity of juvenile European catfish. We assumed that (1) level of activity decreases with increasing body mass, because large individuals are typically dominant and thereby exposed to lower social stresses, (2) familiar individuals will be more active because familiarity often reduces stress and prolongs resource exploitation, (3) the activity of residents will be reduced in the presence of intruders according to stress-induced intrusion, and (4) shelters are highly valuable resources; hence, their availability results in decreased activity.

Materials and methods

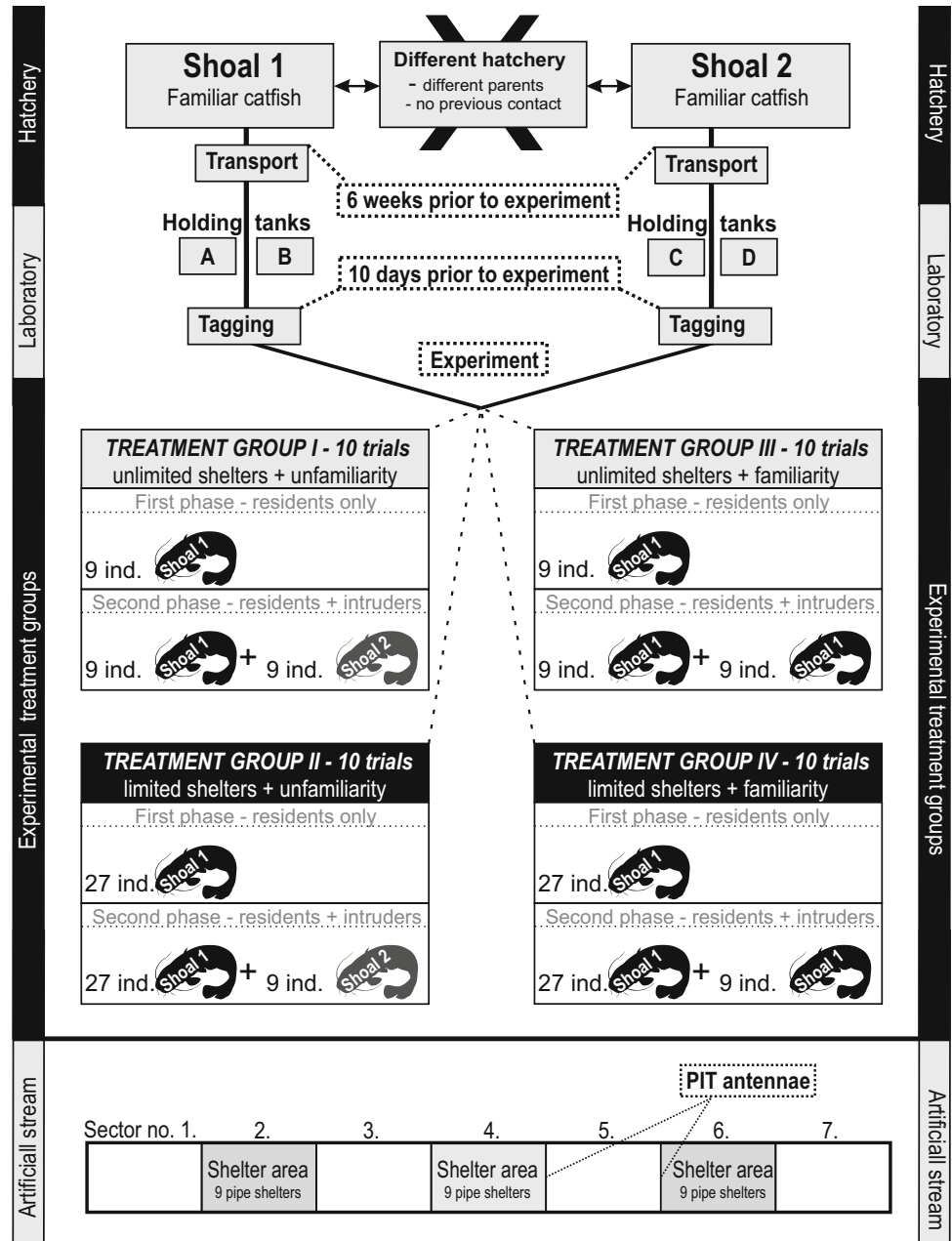
Study organisms used

The experiment was prepared and conducted according to valid legislative regulations (Law no. 246/1992, § 19, art. 1, letter c, filed with permit no. 26758/ENV/10-1092/620/10-PP6, registered by the Ministry of Environment of the Czech Republic). The fish used in the experiment were hatchery-reared juvenile catfish. Two shoals of European catfish unfamiliar with each other were obtained from different local fish suppliers (the first shoal from the Czech Fishery, Rybářství Třeboň, and the second shoal from the Rybářství Nové Hrady, Czech Republic) to ensure that the individuals belonging to the distinct shoals had never been in contact. A total of 1600 equal-sized fish (800 from each shoal) were transported from the hatcheries to the laboratory at the age of 4 months. The fish were transported under stable conditions in oxygenated tanks in an air-conditioned loading space, and the transport lasted approximately 2 h. No effect of the transport was found on the health or mortality of the fish.

The fish were subsequently kept in 4 separate holding tanks (1000 L each, initial density 3.8 kg m^{-3} , i.e., 400 individuals per tank) for 6 weeks prior to the start of the experiment. Each holding tank (A, B, C, and D; Fig. 1) contained individual shelters made of pipes (diameter 5 cm; length 20 cm) that were interconnected to form a honeycomb-like structure (for details, see Slavík et al. 2012). All individuals could inhabit their own shelter, as the number of shelters was higher than the number of fish. Hence, the frequency and intensity of aggressive behavior were low, and the experimenter did not need to intervene to prevent the escalation of interactions to injurious fighting. The fish were fed ad libitum on food pellets (Biomar Group, Denmark, <http://www.biomar.com>) distributed across the whole tank, providing free access to food to all individuals twice a day. The fish were kept under a natural photoperiod, maintaining the same regime to which they had become accustomed in the hatchery. The water was purified using biological filters with an integrated UV steriliser (Pressure-Flo 5000; Rolf C. Hagen, <http://www.lagunaponds.com>). The water temperature, dissolved oxygen and pH were controlled automatically (HOBO data logger; Onset Computer, Bourne, MA, USA).

The fish were tagged 10 days prior to the start of the experiment. The fish were anaesthetised with 2-phenoxyethanol (0.2 ml L^{-1} ; Merck KGaA, Germany) and then measured (standard length LS; mean 102 mm, range 84–128 mm) and weighed (mean body mass 9.6 g, range

Fig. 1 Experimental design and the artificial stream. Repetitions of trials involved the regular rotation of European catfish *Silurus glanis* (L.) from different holding tanks used as residents or intruders to minimise the ‘fish origin’ effect on the results



4–18 g). No size differences between the shoals of fish were detected (standard length $p > 0.87$, $n = 1600$; body mass $p > 0.71$, $n = 1600$). Passive integrated transponders (PIT; Trovan ID 100, 0.1 g in air, 12 mm 2.1 mm; EID Aalten, Aalten, Netherlands) were inserted into the abdominal cavity using a syringe. This method has been successfully used in behavioural experiments (Alanära et al. 2001). No adverse effects of PIT implantation or anesthesia were observed.

All experimental fish (1600 individuals) survived, and, after the experiment, fish were released under the control of Fish Management Authorities into the fish ponds with extensive production management.

Experimental design

The laboratory experiment was conducted between September 1 and December 6, 2011, in an oval artificial stream (see Slavík et al. 2011 for details). For the purpose of this experiment, only one-half of the stream was used (5.25 m long, 0.49 m wide and 0.32 m deep). This segment was divided into 7 subunits using 8 equidistant PIT antennae. A set of 9 interconnected pipe shelters was placed within 3 of the 7 subunits in an alternating pattern (a no-shelter unit followed by a shelter unit and so on; Fig. 1). Pipe shelters have been shown to be an important resource for juvenile catfish (Slavík et al. 2012). We simulated

natural stream conditions in terms of opportunities to swim freely around the shelters, even if they were occupied. We were unable to distinguish between a fish that was directly within a shelter and a fish that was simply near the shelter. Mesh was placed over the outer antennae to prevent fish from escaping from the observed stream segment. The antennae (inner area 0.49 m × 0.25 m) were designed to serve as frames to detect fish swimming through them. The antennae were connected to a recorder that stored the detection information (PIT tag code, date, time and antenna number) in its internal memory. The handling conditions were comparable to those in the holding tanks, and the water quality and flow were controlled by 2 Pressure-Flo 5000 units (60 L/min each). This arrangement generated a visible current (0.01 m s⁻¹) circulating through the stream; however, the fish did not have to swim continuously to maintain their positions. The average temperature, dissolved oxygen content, pH, and conductivity throughout the entire experiment were 19.51 ± SD 0.22 °C, 6.53 ± SD 0.18 mg L⁻¹, 7.24 ± SD 0.14, and 307 ± SD 5.4 μS cm⁻¹, respectively.

To classify ‘prior residency’, 2 phases that were identical for all treatment groups were defined. In the first phase, individuals considered to be ‘residents’ were released into the artificial stream and left there for the following 24 h (beginning at 0800 hours). The data from the first phase of the experiment were not used for further analyses. In the second phase, other individuals considered to be ‘intruders’ were introduced into the artificial stream. The second phase was the experimental phase and lasted for the following 24 h. Different ‘environmental factors’ were defined by the number of available shelters in the artificial stream (resource availability). In the unlimited shelter availability treatment group, there were 27 pipe shelters and 18 individuals (9 first phase + 9 second phase) in the artificial stream, whereas in the limited shelter availability treatment group, there were 27 pipe shelters and 36 individuals (27 first phase + 9 second phase). In each trial, the repetitions were performed by regularly rotating fish from different holding tanks as residents or intruders to minimise the ‘fish origin’ effect on the results. Individual fish were not used in the experiment repeatedly. In the familiar treatment group, the individuals added during the second phase of the experiment as intruders were familiar with the residents (i.e., they were all from the same shoal and holding tank); in the unfamiliar treatment group, they were not. Combining the different features led to 4 experimental treatment groups (Fig. 1), each of which was repeated ten times. Forty individual trial repetitions under the different ecological and familiarity conditions were conducted, resulting in the use of 1080 catfish during the entire experiment. In total, we logged over 3 million recordings of catfish movements. Subsequently, the data

were reduced to a dataset containing 1080 data points (one activity value per each individual fish per 24 h, see below). These data were used in the final statistical analyses.

Statistical analyses

Statistical analyses were performed using R software v.2.11.1 (R Development Core Team, Vienna, 2010). First, the PIT transmitters were used to obtain a raw data sample consisting of more than 3 million separate measurements, each of which included the ID number of the antenna, the ID number of the fish passing through that antenna, and the time. Additional explanatory variables were used to document necessary information on each trial setting (trial repetition, resource availability, familiarity, and prior residency), a fish-specific characteristic (body mass), and certain characteristics based on the individual and the opposite group (for example, the ratio between the individual’s body mass and the mean body mass of individuals from the opposite group). These data introduced unbalanced and irregular longitudinal time profiles for every individual catfish. These profiles were used to compute a total number of antennae passes per each minute based on a one-minute grid. These values (i.e., 1440 values within 24 h) were averaged for each individual to obtain the ‘individual movement activity’ value, one per subject. The individual movement activity was used as a dependent variable. The grid averaging step excludes the dependence occurring within repeated measurements. Additionally, the 1-min grid was chosen as optimal to stabilise the variance and to normalise the data.

Several different modelling approaches were tested. The GLM regression modelling framework was then applied, and a model for Gaussian data with a logarithmic link was proposed. We used the logarithmic link rather than transforming the response using logarithms to preserve the original interpretation of the activity. The final model was selected from other competing models (all two way interactions were tested) always according to a better Akaike’s Information Criterion (AIC) value considering the model with lower AIC to fit the data better (Burnham and Anderson 1998). The AIC of the final model was 27.5 and the range of the ΔAIC comparing it’s fit with other models was 7.3–58.9.

The final model had the following form:

$$\log[\text{EIMA}] = \mu + \Delta_S + \phi_F + \alpha_N + \omega_1 \times \log[\text{BodyMass}] + \omega_2 \times \text{grMeanBodyMass} + [\Delta \times \alpha]_{S \wedge N}$$

where EIMA is an Expected Individual Movement Activity value predicted by the model. The parameter μ is an intercept term for the reference category (unlimited shelters, resident fish and unfamiliarity). Additional intercept

corrections for non-reference categories are introduced via, Δ_S , ϕ_F and α_N . The model also introduces 2 slope parameters, ω_1 and ω_2 , to express a dependence on the logarithm of the individual's body mass 'log[BodyMass]' and the ratio between the individual's body mass and the mean body mass of the individuals in the opposite group 'grMeanBodyMass'. The interaction term $[\Delta \times \alpha]_{S \wedge N}$ between shelter availability and prior residency corrects for the intercept term if the model refers to an intruder under the limited-shelter treatment group. The parameter estimates, together with the standard error estimates and the appropriate significance tests (classical t test p values common for the GLM framework), are given in Table 1. All other explanatory variables considered by the experiment but not listed in the table (for example, a factor covariate for trial repetitions) that were tested in the model building stage as non-significant or did not improve model fit according to AIC were removed from the table.

Results

The expected individual catfish movement activity was dependent on familiarity, prior residency, and body mass as well as on the resource availability (Table 1; Fig. 2). Unfamiliar fish and intruders displayed a higher level of movement activity than familiar conspecifics and residents, i.e. familiarity and prior residency decreased the movement activity of the juvenile catfish. Movement activity generally increased under the resource availability of unlimited shelters; however, the movement activity of residents and intruders differed. The model predicted a slightly lower level of movement activity in residents than in intruders. Moreover, if the shelters were limited, this difference increased significantly to a value 1.5 times greater than that associated with unlimited shelters (Table 1; Fig. 2), i.e. n intruders further increased their activity compared with residents if the shelters were limited. Nevertheless, the movement activity of the fish was also significantly

influenced by body mass and the ratio between an individual's body mass and the mean body mass of the fish from the opposite group (see also Fig. 2). If a catfish was substantially larger than the mean body mass of the opposite group, its movement activity decreased to the minimum irrespective of the ecological conditions, familiarity, and prior residency. Conversely, we observed that the smaller an individual was relative to the mean body mass of the opposite group, the higher the influence of the treatment group was on its activity.

Discussion

In the present study, laboratory observations were used to demonstrate differences in the movement activity of juvenile catfish facing stressful social and environmental conditions. The results showed that when a catfish is substantially larger than the mean body mass of the opposite group, the movement activity of the catfish is decreased to the minimum, irrespective of the social and environmental conditions. We speculated that the social and environmental factors were weak, facilitating the manifestation of individual differences with respect to the behavioural syndromes theory (Sih et al. 2003; Carter et al. 2013). Considering that a low level of movement activity represents success in competition for shelters, lower movement activity with higher body mass supports this assumption. Activity was associated with boldness (Brodin 2008; Conrad et al. 2011), and considering the fact that bold individuals grow faster (Koolhaas et al. 1999), are in better condition (Brown et al. 2007), and reach higher social status (Dahlbom et al. 2011), large catfish can be suggested as bold individuals in the present study. In contrast, smaller conspecifics with a higher level of activity might represent reactive individuals that are more sensitive to stress (Øverli et al. 2005). These results indicate that high body mass, presumably interconnected with boldness and dominance, suppresses reactions to external factors and affect the

Table 1 Parameter estimates with corresponding standard errors and p values for the model

Parameter description	Non-reference category	Model notation	Parameter estimate	Standard error	p value of the test
Intercept	–	μ	–2.3313	1.3267	0.0792
Shelter availability	Limited shelters	Δ_S	–0.6339	0.0946	$0.35 e^{-10}$
Residency	No	α_N	0.6814	0.0755	$<e^{-16}$
Social familiarity	Familiar	ϕ_F	–0.1614	0.0481	0.0008
Log[body mass]	–	ω_1	0.9394	0.2945	0.0015
grMeanBodyMass	–	ω_2	–1.2788	0.2961	$1.73 e^{-5E}$
Shelter availability \times residency	Limited shelters and intruders	$[\Delta \times \alpha]_{S \wedge N}$	0.4115	0.1152	0.0004

Parameter estimates are given by maximum likelihood estimation and p values are obtained using a classical t test common for GLM regression framework

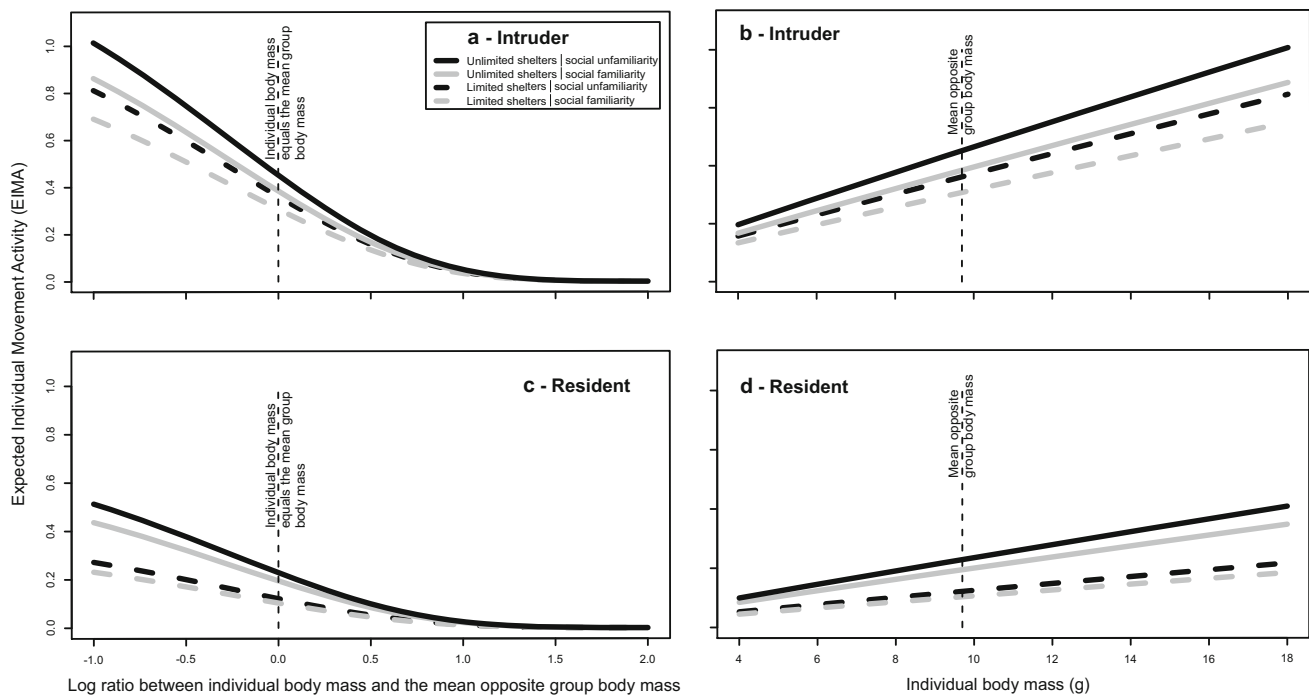


Fig. 2 Expected individual movement activity (EIMA) values plotted against the logarithm of the ratio between individual body mass and the mean opposite group body mass (a) and individual body mass (b) for intruders and, analogously, for residents (c, d). Four different treatment groups are distinguished (unlimited shelters, unfamiliarity

black solid line; unlimited shelters, familiarity grey solid line; limited shelters, unfamiliarity black dashed line; limited shelters, familiarity grey dashed line). A vertical line is plotted for a ratio equal to zero. This value indicates that the individual's body mass equals the mean body mass of the opposite group

results of competition. This effect is strong, particularly in combination with the motivation to defend a valuable territory (Stokkebo and Hardy 2000; Kokko et al. 2006), represented by shelter availability in this case.

Despite information that familiarity typically increases movement activity (Liebgold and Dibble 2011), the results showed that familiarity predicted low movement activity. This finding corresponds with previous studies showing that familiar fish more effectively exploit resources (Höjesjö et al. 1998; Griffiths et al. 2004), because the recognition of social partners facilitates the avoidance of ineffective time and energy use, injury, and/or predation risk (Giraldeau and Caraco 2000; Griffiths and Ward 2011). Correspondingly, the familiarity of juvenile catfish has been associated with low movement activity resulting from the advantageous characteristic of the recognition of social partners in a group. Furthermore, the results showed that the asymmetric relationship between resident and intruder was associated with differences in movement activity, indicating a lower level of movement activity of residents with no respect to changes in resource availability during the experiment, expressed as shelter limitation. Thus, resource limitation plays a fundamental role in processes in natural systems (Murdoch 1994; Turchin 1999), and its direct influence is associated with a critical degree of resource saturation (Osenberg et al. 2002). Shelters also

represent highly contested resources (Sultana et al. 2013). Ford and Swearer (2013) showed that shelter limitation was the best predictor of mortality in coral reef fish. In the present study, we examined the effect of shelter limitation as a saturated critical resource of the activity of catfish. Unlimited shelter availability induced higher movement activity in juvenile catfish. Note that experimental animals typically display an initially intensive response to a novel environment, with subsequent habituation and a gradual decline in activity (Gómez-Laplaza and Morgan 2003). In contrast, the tendency of the intruders to further significantly increase activity compared with residents when the per capita availability of shelters is low suggests that intruders also show increased activity resulting from unfavourable environmental conditions. As reported, residents are predicted to prevail in defence of highly valuable territory (Stokkebo and Hardy 2000; Humphries et al. 2006; Gherardi 2006; Takeuchi 2006). Because per capita shelter availability was the only variable environmental condition in the present experiment, we speculated that residents succeed in defence of valuable territories, i.e. the residents are more invested in shelter defence, whereas intruders are more invested in searching for shelter. This investment by the intruders has been associated with higher movement activity. The lower movement activity of residents can also be considered in terms of differences in

status in the social hierarchy. For example, Rosell et al. (2008) reported the over-domination of resident root vole *Microtus oeconomus* males in pairwise interactions. In the present study, we observed asymmetry in the movement activity of residents and intruders: the residents showed a lower level of activity, which might represent successful territorial defence. Although the outcome of competition for resources is affected by the complexities of the various factors with less apparent structure (Kokko et al. 2006), the results indicated that competition is accompanied by a lower level of movement activity by residents than by intruders.

Thus, the results presented here are consistent with previous studies describing the relationship between social experience and animal behaviour. Correspondingly, as familiarity is beneficial for resource exploitation, we recorded a lower movement activity of familiar catfish needed for shelter occupancy. Furthermore, the asymmetric relationship between residents and intruders was accompanied by differences in movement activity, with a lower level of movement activity shown by the residents. These findings are consistent with theories predicting the success of residents defending their territories when using the advantage of prior residency and higher motivation for the defence of valuable resources. These social (familiarity/unfamiliarity, resident/intruder) and environmental factors (resources availability) have been suggested as weak, demonstrating individual differences represented as body mass. High individual body mass predicted low movement activity, irrespective of the social and environmental conditions. Thus, the results of the present study highlight a role for individual characteristics in shaping the behavioural responses of catfish to external factors.

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How does agonistic behaviour differ in albino and pigmented fish?

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ABSTRACT

In addition to hypopigmentation of the skin and red iris colouration, albino animals also display distinct physiological and behavioural alterations. However, information on the social interactions of albino animals is rare and has mostly been limited to specially bred strains of albino rodents and animals from unique environments in caves. Differentiating between the effects of albinism and domestication on behaviour in rodents can be difficult, and social behaviour in cave fish changes according to species-specific adaptations to conditions of permanent darkness. The agonistic behaviours of albino offspring of pigmented parents have yet to be described. In this study, we observed agonistic behaviour in albino and pigmented juvenile *Silurus glanis* catfish. We found that the total number of aggressive interactions was lower in albinos than in pigmented catfish. The distance between conspecifics was also analysed, and albinos showed a tendency towards greater separation from their same-coloured conspecifics compared with pigmented catfish. These results demonstrate that albinism can be associated with lower aggressiveness and with reduced shoaling behaviour preference, as demonstrated by a tendency towards greater separation of albinos from conspecifics.

Subjects Animal Behavior, Aquaculture, Fisheries and Fish Science, Zoology

Keywords Albinism, Siluriformes, Catfish, Pleiotropic effect, Aggressive and Mobile display

INTRODUCTION

Albinism is generally the result of combinations of homozygous recessive mutations from pigmented parents, and in particular, albinos are often unable to synthesize tyrosine and melatonin hormones ([Carden et al., 1998](#)). This disability is not only associated with red irises and light skin colouring (oculocutaneous albinism, OCA; [Carden et al., 1998](#)) but also with physiological, behavioural and social alterations. Some of vertebrate albinisms are indeed associated with increased levels of tyrosine and catecholamine accompanying with physiological and behavioural changes that occur during adaptation to specific conditions in caves ([Bilandžija et al., 2013](#)).

Information on the prevalence of terrestrial albino animals in the wild is primarily based on reports, and information on social interactions between albinos is mostly limited to studies of specially bred strains of albino rats, whose behaviour is strongly influenced by domestication ([Himmeler et al., 2014](#)). The eyes of albino rodents show reduced adaptation to light, often leading to photoreceptor degradation ([Prusky et al., 2002](#); [Refinetti, 2007](#); [Marc et al., 2008](#)), which in turn can cause loss of vision ([Buhusi, Perera & Meck, 2005](#)) and movement perception ([Hupfeld & Hoffmann, 2006](#)), eventually leading to acrophobia

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and/or photophobia ([Abeelen & Kroes, 1967](#); [Owen, Thiessen & Lindzey, 1970](#)). Albino rodents have a poorer sense of smell ([Keeler, 1942](#)) and display lower activity levels compared with pigmented conspecifics ([Fuller, 1967](#); [DeFries, 1969](#)). In particular, their activity is low during the day and increases during the night ([Stryjek et al., 2013](#)). Albino rats also spend longer periods in deep sleep (rapid eye movement, REM), especially during the dark phase ([Benca, Gilliland & Obermeyer, 1998](#)), and during the night, they sleep more often out of the nests relative to pigmented conspecifics ([Stryjek et al., 2013](#)). Albino rats are slower to inhibit the fear response and explore new objects ([Pisula et al., 2012](#)), and they are less effective in completing spatial tasks ([Harker & Whishaw, 2002](#)). For example, albino rats displayed higher hoarding activity ([Rebouças & Schmidek, 1997](#)), and they burrowed more slowly and constructed less complex systems of tunnels compared with wild conspecifics ([Stryjek, Modlińska & Pisula, 2012](#)).

Furthermore, albino vertebrates can be found in water environments, and compared with pigmented conspecifics, they display physiological and behavioural differences. For example, blind tetra *Astyanax mexicanus* (De Filippi 1853) living in caves ([Jeffery, 2001](#)), compared with the pigmented surface-dwelling form, display physiological adaptations to permanent darkness and limited food availability, such as greater number of taste buds ([Yamamoto et al., 2009](#)) and highly sensitive sensors in the lateral line ([Yoshizawa et al., 2010](#); [Yoshizawa, O'Quin & Jeffery, 2013](#); [Yoshizawa et al., 2014](#)). Such physiological adaptations appear to have resulted in a decrease in the length of sleep ([Duboué, Keene & Borowsky, 2011](#)), loss of schooling behaviour ([Kowalko et al., 2013](#)), and an evolutionary shift from fighting to food source searching, leading to the loss of hierarchy dominance and aggressiveness ([Elipot et al., 2013](#)). On the contrary, blind albino catfish in caves displayed agonistic behaviour ([Parzefall & Trajano, 2010](#)) likely reflecting their relatively large body size and bottom-dwelling form associated with stronger competition for resources. For example, the catfish *Pimelodella kronei* (Ribeiro 1907) showed a similar level of aggressiveness to its pigmented and sighted ancestor *Pimelodella transitoria* (Ribeiro 1907; [Trajano, 1991](#)).

Albinism in catfish often occurs in surface waters as well ([Dingerkus, Seret & Guilbert, 1991](#); [Britton & Davies, 2006](#); [Wakida-Kusunoki & Amador-del-Angel, 2013](#); [Leal et al., 2013](#)). [Slavík, Horký & Maciak \(2015\)](#) described the separation of albino *Silurus glanis* (Linnaeus 1758) catfish from a group of pigmented conspecifics. The irregularity of albinos in a group of pigmented conspecifics means a guiding target for predators ([Landeau & Terborgh, 1986](#); [Theodorakis, 1989](#)), facilitating their hunting ([Ellegren et al., 1997](#)), and may be a reason for exclusion of albinos from a group ([Slavík, Horký & Maciak, 2015](#)). However, it is not yet clear whether albinism in animals is associated with alternative social behaviour, resulting in for example, ostracism. A possible alternative behavioural display is a shift in aggression altering e.g., between domesticated albino rodents and their wild ancestors and/or between troglobites and their pigmented surface-dwelling counterparts. In the present study, we observed aggressiveness in albino and pigmented catfish *Silurus glanis* from surface waters. Considering the generally lower level of aggression observed in albino animals, we assumed that agonistic behaviour would be lower in albinos than in pigmented conspecifics.

MATERIALS & METHODS

Albinism in catfish *Silurus glanis* L. 1758 has been commonly recorded in the wild (*Dingerkus, Seret & Guilbert, 1991*), where catfish usually occur in groups (*Boulétreau et al., 2011*). Only juvenile catfish were used to reflect the behaviour of wild fish. These juveniles were spatially separated from adults (*Slavík et al., 2007*), and showed complex social behaviours under the experimental conditions (*Slavík, Maciak & Horký, 2012; Slavík et al., 2016*).

Experimental animals

The fish used in this experiment were hatchery-reared juvenile catfish. One shoal of pigmented and one shoal of albino catfish that were unfamiliar to each other were obtained from local fish suppliers (Czech Fishery Ltd., Rybářství Hluboká and Rybářství Třeboň, Czech Republic, respectively). A total of 400 approximately equally sized fish (200 from each shoal) were transported from the hatcheries to the laboratory at four months of age. The fish were transported under stable conditions in oxygenated tanks in an air-conditioned loading space. Transport lasted approximately 2 h, and there were no observable effects on the health or mortality of the fish.

The fish were maintained in two separate holding tanks (380 L each, initial density 1.9 kg m^{-3} ; one shoal or 200 individuals per tank) for eight weeks prior to the start of the experiment. The fish were fed food pellets ad libitum (Biomar Group, Denmark, www.biomar.com) that were distributed throughout the entire tank, providing free access to food to all individuals twice a day. The fish were maintained under a natural photoperiod, which was the same regime they had become accustomed to in the hatchery. The water was purified using biological filters with an integrated UV sterilizer (Pressure-Flo 5000; Rolf C. Hagen Inc., www.lagunaponds.com). The water temperature and dissolved oxygen were controlled automatically (HOBO data logger; Onset Computer Corporation, Bourne, MA, USA). Fish were measured (mean 103 mm; range 90–117 mm) and weighed (mean 10 g, range 6–15 g) at the end of the experiment and removed to separate tanks to prevent mixing with unused conspecifics.

All experimental fish (400 individuals) survived. After the experiment, the fish were released under the control of the Fish Management Authorities into fish ponds with extensive production management.

Experimental design

The experiment was conducted in the laboratory between December 2013 and January 2014. A pair of randomly selected individuals of the same colour was placed into a rectangular plastic experimental arena (36 cm long, 18 cm wide, 20 cm high) at the beginning of each trial. The arena was separated by a partition into two equal parts, and the individuals were placed on opposite sides of the arena. After an acclimation period of 1 min, the partition was removed and the behaviour of the fish was recorded for 5 min using a digital camera (GoPro Hero; GoPro, Inc., San Matteo, CA, USA). The arena was flushed out and filled with clean water after every trial. In total, 40 trials (20 pairs of albinos and 20 pairs of pigmented individuals) were conducted.

Data analysis

In the laboratory experiment, we tested two levels of aggressive interactions among juvenile catfish, designated as aggressive or mobile displays (Lehtonen, 2014). Aggressive displays were further subdivided into frontal and lateral displays, and mobile displays were further subdivided into chasing and biting displays (Hsu & Wolf, 1999; Dijkstra et al., 2009). The sum of aggressive interactions, referred to as ‘total aggression,’ was used in further analyses (Pauers et al., 2012). The bottom of the experimental arena was divided into six equally sized squares (9×12 cm) that were used in the analyses of ‘mutual distance.’ Mutual distance was set as a three level class variable. A mutual distance equal to 1 meant that the individuals were in the ‘same zone,’ meaning that both conspecifics were in the same square. A mutual distance equal to 2 meant that the individuals were in ‘adjacent zones,’ meaning that conspecifics were in adjacent squares. A mutual distance equal to 3 meant that the individuals were in the ‘farthest zones,’ meaning that there was one square between conspecifics. Variable ‘size difference’ was defined as the difference between the weights of two interacting conspecifics in an experimental arena (mean 1.9 g; range 0–6 g). For the purpose of analysing the probability of occurrence of different types of agonistic behaviour over time, a ‘time grid’ of 5 s was set. For every time grid value, the probability of occurrence of a particular agonistic behaviour was recorded as 1 (behaviour occurred) or 0 (behaviour did not occur). The EthoLog software program (<http://www.ip.usp.br/docentes/ebottoni/EthoLog/ethohome.html>) was used to assign the number of particular agonistic behaviours as well as the ‘duration’ (in seconds) that conspecifics spent at particular mutual distances.

Statistical analysis

Statistical analyses were performed using the SAS software package (version 9.2; SAS Institute Inc., Cary, NC, USA). When necessary, the data were square root transformed to meet normality requirements.

Total aggression and duration were analysed using mixed models with random factors (PROC GLIMMIX with Poisson distribution for total aggression and PROC MIXED with normal distribution for duration). Random factors were used to account for repeated measures collected for the same experimental units (pair of conspecifics) across the duration of the experiment. The significance of each exploratory variable (i.e., fixed effects, including their interactions) in the particular model was assessed using an F-test in which we sequentially dropped the least significant effect, beginning with the full model (backward selection procedure). Least-squares means (LSM), henceforth referred to as “adjusted means,” were computed for class variables. The differences between the classes were tested using a *t*-test, and a Tukey–Kramer adjustment was used for multiple comparisons. The degrees of freedom were calculated using the Kenward–Roger method (Kenward & Roger, 1997).

The probabilities of occurrence for particular agonistic behaviours were analysed using the generalized estimating equation (GEE) approach (Liang & Zeger, 1986) for categorical, repeated measurements using the GENMOD procedure with binomial distributions. This approach is an extension of generalized linear models that provides a semi-parametric approach to longitudinal data analysis. In this study, four separate GENMOD procedures

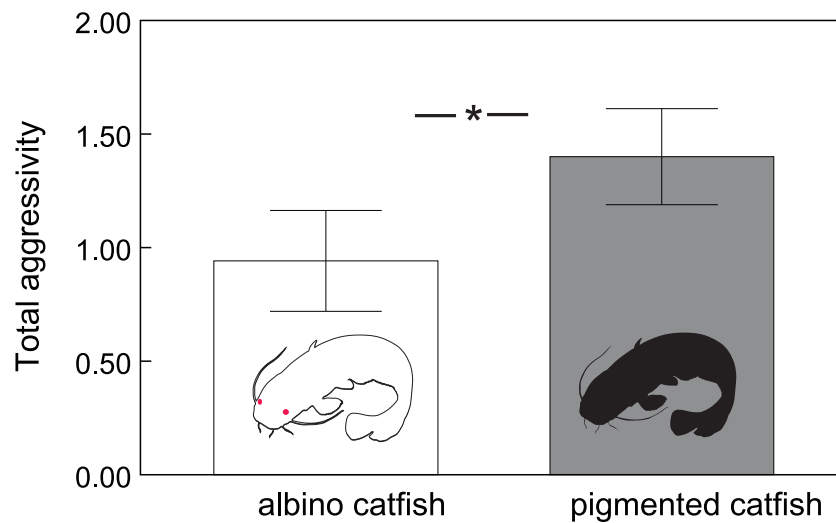


Figure 1 Total number of aggressive interactions (adjusted means \pm SE) across albino and pigmented treatments. Significant differences are indicated (*; Tukey–Kramer adjusted $P < 0.0002$).

were designed to estimate the probability of occurrence of particular agonistic behaviours (i.e., chasing, biting, frontal and lateral displays) across the duration of the experiment.

Ethics statement

All of the laboratory experimental procedures were in compliance with valid legislative regulations (law no. 246/1992, § 19, art. 1, letter c). The permit was granted to O. Slavík, according to Law no. 246/1992, § 17, art. 1; permit no. CZ00167. All laboratory samplings were conducted with the permission of the Departmental Expert Committee for Authorization of Experimental Projects of the Ministry of Education, Youth and Sports of the Czech Republic (permit no. MSMT-31220/2014-6). This study did not involve endangered or protected species.

RESULTS

In total, we observed 1208 aggressive interactions, 68% of which were classified as lateral displays, 16% as frontal displays, 11% as chasing displays and 5% as biting. The total number of aggressive interactions was lower in the albino group ($F_{1,110.6} = 14.51$, $P < 0.0002$; Fig. 1). In addition, the probability of chasing ($\chi^2 = 6.64$, d.f. = 2; $P < 0.0362$; Fig. 2A) and lateral display ($\chi^2 = 6.04$, d.f. = 2; $P < 0.0488$; Fig. 2B) changed over time and differed between groups. In the albino group, the probability of chasing decreased over time, whereas the probability of lateral display did not show any significant trend. In the pigmented group, the probability of chasing also decreased over time, whereas the probability of lateral display sharply increased. In neither group did the probability of frontal display or biting vary significantly over time. The results indicated that albinos were less aggressive compared with their pigmented conspecifics, which was primarily due to a higher probability of lateral display behaviours in the pigmented group.

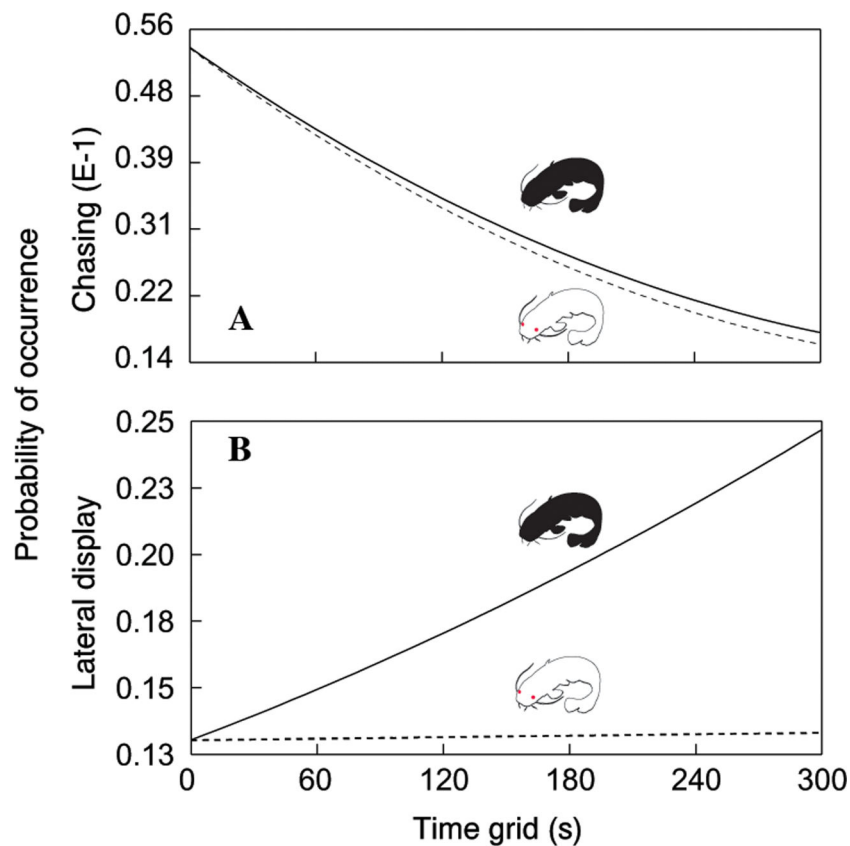


Figure 2 Probability of chasing (A) and lateral display (B) as a function of time across the two treatments. Dotted line = albino catfish; black line = pigmented catfish.

Furthermore, the time that conspecifics spent at a particular distance from other conspecifics varied in both groups ($F_{5,111} = 29.43$, $P < 0.0001$; Fig. 3). While the catfish (both albino and pigmented) generally spent the least amount of time in the farthest zones (time spent in the farthest zones did not differ between albino and pigmented catfish), albinos spent more time in adjacent zones and less time in the same zones than pigmented conspecifics (Adj. $P < 0.05$). Taken together, we found that albino catfish showed a higher tendency to be spatially separated from conspecifics, whereas pigmented catfish showed a tendency towards close contact.

DISCUSSION

The assumption that albinism is associated with different levels of aggression is supported by this study. In particular, our results support the theory that species with different levels of colouration should display different levels of aggression (Pryke & Griffith, 2006) and that the level of aggression should correspond to different colour morphs (Pryke, 2009; Dijkstra et al., 2009). Indeed, one colour morph is often predicted to be more aggressive than others (Dijkstra et al., 2010). Our results are also consistent with recent findings showing that albinism has pleiotropic effects that are mediated through hormones that can

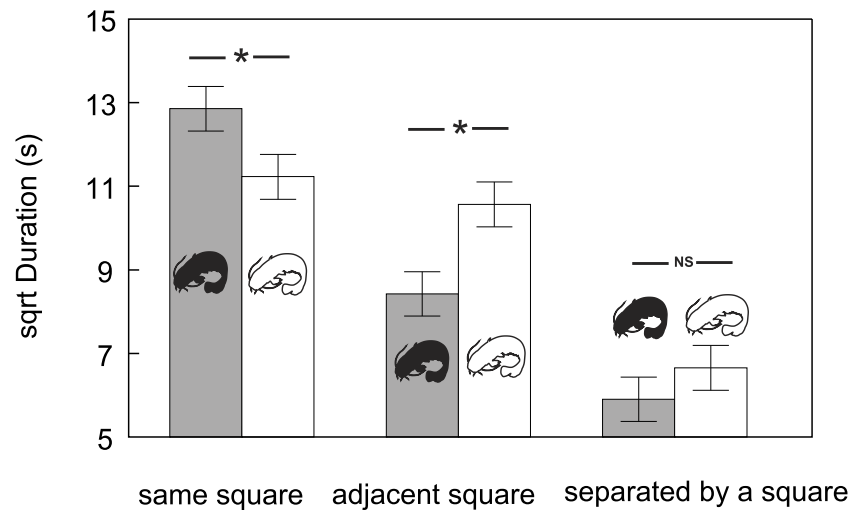


Figure 3 Duration (adjusted means \pm SE of square root data) of time that conspecifics spent at particular mutual distances across albino and pigmented treatments. Significant differences are indicated (*; Tukey–Kramer adjusted $P < 0.05$).

affect both skin pigmentation and aggressive behaviour (Gonzales, Varizi & Wilson, 1996; Ducrest, Keller & Roulin, 2008). As reported by Horth (2003), increases in the aggression of the melanic form of mosquitofish correlate with changes in melanin synthesis. Therefore, albinism, in contrast to melanism, may be generally associated with lower aggression due to shared genetic control mechanisms.

Comparison of the pigmented and albino forms of *Silurus glanis* revealed lower aggressiveness in albinos. Loss of aggressive behaviour has been reported for albinos living in caves (Elipot et al., 2013), and this relationship tend to be related to species-specific adaptations to unique environmental conditions. For example, most of the populations of the blind albino tetra *A. mexicanus* have lost aggressiveness, whereas individuals of the pigmented surface-dwelling form blinded in an early ontogenetic stage remain aggressive at the same level as their sighted parents (Espinasa, Yamamoto & Jeffery, 2005). Blind albino catfish in caves displayed similar aggressiveness to their sighted surface ancestors (Trajano, 1991). According to Espinasa, Yamamoto & Jeffery (2005), aggressive behaviour is activated by non-optical releasers, and the reduction of aggressiveness is not the exclusive evolutionary pathway for blind albino trogllobites. Loss of vision in albino cavefish *A. mexicanus* is accompanied by the development of non-visual sensors, such as neuromasts along the lateral line (Yoshizawa et al., 2010; Yoshizawa, O'Quin & Jeffery, 2013; Yoshizawa et al., 2014). Similarly, catfish are not typical visual predators such as salmonids (Valdimarsson & Metcalfe, 2001), but are adapted to prey detection in lowland rivers with a high level of turbidity, where prey are often hunted during flash floods (Slavík et al., 2007). Six robust tactile bristles are used for prey detection in these catfish, and with the aid of highly sensitive lateral line, the species can detect hydrodynamic traces as long as 10 s after the passage of prey (Pohlmann, Grasso & Breithaupt, 2001). Provided that the vision of pigmented catfish does not represent the main tool for prey detection,

it can be inferred that its role in the aggressive behaviour of albino catfish *S. glanis* is also minor. Although it can be assumed that albino catfish from surface waters are able to see, their vision may be impaired. Accordingly, albinism in mice has been correlated with acrophobia, photophobia and lower visual acuity ([Owen, Thiessen & Lindzey, 1970](#); [Prusky et al., 2002](#); [Buhusi, Perera & Meck, 2005](#)). Moreover, specially bred strains of albino rats (Sprague-Dawley) displayed a higher probability of playful attacks compared with wild-type pigmented strains ([Himmler et al., 2014](#)). The behaviour of this Sprague-Dawley strain, however, was also different from other albino strains. Interestingly, the authors attributed these differences to differing levels of domestication in each of the strains. Playful attacks are associated not only with domestication (see review [Himmler et al., 2014](#)) but also with reduced aggression, as albino rats are less aggressive than their wild-type pigmented counterparts ([Barnett, Dickson & Hocking, 1979](#); [Barnett & Hocking \(1981\)](#)). Although a direct comparison between aggressiveness in catfish and rats is not possible, we speculate that albinism may be generally associated with lower aggression compared with normally pigmented conspecifics.

Aggression is also associated with social position or rank ([Mazur & Booth, 1998](#); [Staffan, Magnhagen & Alanärä, 2002](#)). For example, an albino female vampire bat *Desmodus rotundus* bred with pigmented individuals hold the lowest social position ([Uieda, 2001](#)). Hence, albinism may be associated with not only lower aggressiveness but also lower dominance, as these characteristics are often correlated ([Dijkstra, Seehausen & Groothuis, 2005](#); [Pryke & Griffith, 2006](#)). Indeed, consistent with this idea, ostracism of albino catfish by a group of pigmented conspecifics has been described ([Slavík, Horký & Maciak, 2015](#)), and the low ability of albinos to remain within a group may be another reason for the high predation risk in albinos ([Ellegren et al., 1997](#)).

Albino catfish also showed a greater tendency towards spatial separation compared with their pigmented conspecifics, which preferred to be nearer to one another. This finding differs from what was observed in domesticated albino rats, which were found to be more tolerant of conspecifics compared with wild-type strains ([Himmler et al., 2013](#); [Himmler et al., 2014](#)). Indeed, colour-assortative shoaling is often observed ([McRobert & Bradner, 1998](#); [Spence & Smith, 2006](#); [Goméz-Laplaza, 2009](#); [Rodgers, Kelley & Morell, 2010](#)). Considering the fact that albino catfish are unable to darken their body colour to avoid aggressive interactions with dominant conspecifics ([O'Connor, Metcalfe & Taylor, 1999](#); [Höglund, Balm & Winberg, 2000](#)), spatial separation may be a strategy for avoiding the escalation of aggressive behaviours. On the other hand, if albino catfish have poor vision, then their low tendency towards grouping may be a result of this weakened physiological condition. Accordingly, blind cave fish displayed loss of schooling behaviour ([Parzefall & Trajano, 2010](#); [Kowalko et al., 2013](#)). In the case of troglobites, however, a low tendency towards grouping is considered to represent an evolutionary adaptation to sparse prey and low food availability, conditions where life in a group is not beneficial to better foraging activity such as it is in surface waters ([Griffith et al., 2004](#); [Ward & Hart, 2005](#)). Large numbers of albinos existing together in the wild has only been reported in insects ([Hoste et al., 2003](#)), and whether albinos are mutually attracted to each other and form larger groups in nature remains unknown.

CONCLUSIONS

Similarities to the shift in the behaviour of albino catfish towards lower aggressiveness can be found in domesticated albino rodents and their wild pigmented counterparts as well as between blind cave fish and their sighted ancestors from surface waters. Therefore, loss of pigmentation may not only be linked to aggression in albinos, but also have other pleiotropic effects that can be observed, for example, as impaired eyesight in surface environments and/or specie-specific evolutionary adaptations to conditions of permanent darkness. In addition, albinos were found to maintain greater distances between themselves compared with pigmented individuals in the present study, corresponding to the loss of schooling behaviour in blind cave fish.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Ondřej Slavík conceived and designed the experiments, performed the experiments, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Pavel Horký conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Marie Wackermannová analyzed the data.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

All of the laboratory experimental procedures were in compliance with valid legislative regulations (law no. 246/1992, § 19, art. 1, letter c). The permit was granted to O. Slavík,

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Data Availability

The following information was supplied regarding data availability:

The raw data has been supplied as Supplemental Datasets.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1937#supplemental-information>.

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Olfactory Sensitivity in Mammalian Species

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Summary

Olfaction enables most mammalian species to detect and discriminate vast numbers of chemical structures called odorants and pheromones. The perception of such chemical compounds is mediated *via* two major olfactory systems, the main olfactory system and the vomeronasal system, as well as minor systems, such as the septal organ and the Grueneberg ganglion. Distinct differences exist not only among species but also among individuals in terms of their olfactory sensitivity; however, little is known about the mechanisms that determine these differences. In research on the olfactory sensitivity of mammals, scientists thus depend in most cases on behavioral testing. In this article, we reviewed scientific studies performed on various mammalian species using different methodologies and target chemical substances. Human and non-human primates as well as rodents and dogs are the most frequently studied species. Olfactory threshold studies on other species do not exist with the exception of domestic pigs. Olfactory testing performed on seals, elephants, and bats focused more on discriminative abilities than on sensitivity. An overview of olfactory sensitivity studies as well as olfactory detection ability in most studied mammalian species is presented here, focusing on comparable olfactory detection thresholds. The basics of olfactory perception and olfactory sensitivity factors are also described.

Key words

Olfaction • Sensitivity • Odor detection threshold • Mammals

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Introduction

Chemosensory systems develop very early in ontogeny and are found in almost every animal. The mammalian sense of smell detects and discriminates between innumerable substances that have very diverse chemical structures and features (Corcelli *et al.* 2010). The omnipresent chemical stimuli enable detection and discrimination of home range, conspecifics, mates, mother, food resources, predators, and prey. Chemosensation is critical for survival and reproductive success (Wilson 2006). Many species use chemical cues to recognize genetically related kin, even the identity of conspecifics using individual olfactory cues in order to avoid inbreeding as well as to determine the animal's reproductive status (Wilson 2006, Cometto-Muniz and Abraham 2008). Olfaction also helps protect the entire organism as this system provides an early warning system for the detection of health hazards and imminent threats (fire, leaking natural gas, rotten food, or toxins) and plays a critical role in nutrition (Laska and Hudson 1993, Hawkes and Doty 2009). The sensory and hedonic

evaluations of most food-related flavors are mainly dependent on olfactory perception (Nevitt 2000).

Chemosensory-based communication is a vital signaling tool (Frasnelli *et al.* 2011). From the most gregarious to the most solitary, all animals need to coordinate their activities with others of the same species. This coordination is based on communication (Laberge and Hara 2004), which involves utilization of chemical signals known as pheromones (sexual attractant pheromones, mammary pheromones, aggression pheromones, alarm pheromones, marking pheromones) (Brennan 2010).

Olfactory sensitivity in mammals has been studied since the 1960s, but experiments focused on an exact olfactory threshold are rare. The small number of these experiments differs in methods as well as in results. The main aim of this review is to present the olfactory thresholds of mammalian species and to show the exclusivity of the olfactory system in mammals, despite the differences in the results of individual studies.

There has been a long-term effort to compare odor perception in humans and animals. The comparison may develop scientific evidence concerning hypotheses about relative olfactory powers in humans and other mammalian species. An important criterion is the integration of human psychophysical results with animal results in similar studies, as animal results may approximate the neural mechanism and olfactory perception in humans (Walker and Jennings 1991).

What is olfaction?

Olfaction mediates the perception of volatile chemicals, which convey information about the environment to the receiver. Variations in the precise structure of individual odorant molecules, concentrations of those molecules, and specific combinations and relative concentrations of components in a mixture of odorant molecules provide crucial information about the surrounding world. Given that most odors are complex mixtures of a number of single components, the discrimination of one odor from another is difficult, and previous experience enhances odor discrimination in mammalian species (Firestein 2001, Croy *et al.* 2015).

Over time, a number of theories have been attempted to explain the relationship between the molecular structure and odor in the primary olfactory reception mechanism. The view of the reception

mechanism evolved from the “lock and key” theories that claim molecular shape determines odor (Wright 1977, Frater 1998) over odotope theory-based identification of receptor subtypes responding not to one but to many odorants (Mori 1994, Malnic *et al.* 1999) to vibration theory (Turin and Yoshii 2003). This theory, based on the molecular vibrations of odorants, was first described in 1938 (Dyson 1938) and has been newly extended by Turin (2002). This theory states that odor is determined by the vibration spectrum of the molecule. The detection mechanism is based on inelastic electron tunneling, and the vibration spectra of the odorants determine their odor (Turin and Yoshii 2003), but after clean chemical deuteration studies (Block *et al.* 2015) the vibration theory should be reexamined (Vosshal 2015). In conclusion, no theory explaining the principles of the odorant-receptor interaction has been proved to be entirely plausible (Zarzo 2007).

Individual variations in the limits of detection for different stimuli have been known for a long time. Although individual odor thresholds vary, studies have indicated the variations within an individual are comparable to variations between individuals (Cain 1989). The olfactory threshold is the minimum concentration of a target stimulus an individual is able to reliably differentiate from a blank sample (deionized water in most studies). In recent experiments that focused on olfactory sensitivity in mammalian species, the olfactory detection threshold (ODT) was considered the limit of olfactory sensitivity.

Olfactory subsystems

In mammals, the olfactory, gustatory, and trigeminal systems are involved in chemical senses (sense of smell, taste, somatosensation). The nose, the main olfactory organ, consists of multiple olfactory subsystems, among which the main olfactory epithelium (MOE) and the vomeronasal organ (VNO) have been the most studied (Trotier 2011). The MOE is composed of two types of cells, microvillar cells and olfactory sensory neurons (OSNs), which express G-protein-coupled odorant receptors. The VNO contains two olfactory subsystems (apical and basal) and two classes of vomeronasal receptors (V1Rs and V2Rs) (Young *et al.* 2010). Although human embryonic VNO exerts a developmental track common to microsmatic mammals, after the initial development, the VNO regresses, with only a few vestiges persisting in adults and most

chemoreceptor cells within the persistent vomeronasal duct (VND) wear off. By the absence of neurons and vomeronasal nerve bundles it can be deduced that the vomeronasal epithelium is not a sensory organ in adult humans (Trotier *et al.* 2000). The genes that code for the V1R-type and V2R-type receptor proteins are mostly nonfunctional in humans (Mohedano-Moriano *et al.* 2008). Although vomeronasal ducts and pits have been observed in humans (Moran *et al.* 1991, Stensaas *et al.* 1991, Boehm and Gasser 1993, Trotier and Doving 1996), evidence of functional vomeronasal receptor neurons connected to the brain has not been found in adult humans (Johnson 1998, Smith *et al.* 2014). In some species, there are two additional spatially segregated clusters of sensory cells, the septal organ (SO) (Storan and Key 2006) and the Grueneberg ganglion (GG), which are particularly well developed in mice (Brechtbuhl *et al.* 2014). Each of the four physically segregated apparatuses can convey sensory information about multiple modalities and serve multiple functions. Although these chemosensory subsystems detect distinct chemical substances, the olfactory cues overlap substantially. No behavioral studies have tested the olfactory subsystems separately, since it is not possible to test only part of the complex olfactory system without an invasive intervention in the subject organism.

Main factors of olfactory sensitivity

An animal's sense of smell enables the animal to recognize and discriminate numerous airborne molecules with great accuracy and sensitivity (Wu *et al.* 2011). The behavioral relevance of an odorant may be an important determinant of a species' olfactory sensitivity (Laska *et al.* 2005a, 2007a, Olsson and Laska 2010, Ferdenzi *et al.* 2013). It has also been determined that olfactory acuity increases during fasting, allowing some mammalian species to detect food and environmental odors, such as those of predators, more easily (Aime *et al.* 2007). The connection between body weight and olfactory sensitivity has been observed in mammals, especially in rats (Thanos *et al.* 2013). Changes in olfactory sensitivity are related to circadian locomotor behavior as well. Odor stimuli can act as a circadian time cue that modulate circadian behavior in mammals (Abraham *et al.* 2013). To utilize chemical cues, animals must have olfactory systems that can deal with at least four specific issues: 1) the detection of the stimulus; 2) discrimination of the stimulus from other potentially very similar stimuli; 3) dealing with and,

perhaps, determining relative stimulus intensity; and 4) assigning meaning to the stimulus (Wilson 2006, Wilson and Mainen 2006). Detection is the degree of presence, while recognition involves matching input, and identification is the assignment of meaning. These three different functions do not necessarily correlate with specific anatomical locations (Mombaerts 2001).

Repeated exposure is an important factor in developing olfactory sensitivity, so learning is evidently a vital part of olfactory perception (Wilson and Stevenson 2003). The synapses and receptive fields of the cerebral cortex are plastic. Modification of cortical inputs leads to synaptic changes, which are related to improved sensory perception and enhanced behavioral performance (Guthoff *et al.* 2009). Not only the olfactory threshold but also the olfactory discrimination of similar odorants (odor acuity) in general can improve with experience (Ferdenzi *et al.* 2013), and the ability to successfully distinguish between similar odorants depends on the specific behavioral response of particular species (Giannaris *et al.* 2002, Wiltrout *et al.* 2003). The role of experience was found even in the prenatal stage in the rabbit (Coureaud *et al.* 2004). Some studies suggested that repeated exposure to an odorant may influence the threshold level. The exposure to either amyl acetate or androstenone in mice leads to enhanced sensitivity (Yee and Wysocki 2001). Conversely, some investigations found that repeated or prolonged exposure to an odorant decreases olfactory sensitivity to that odorant; however, the sensitivity recovers over time in the absence of exposure (Hudson 1999). It seems to be dependent on the concentration of the odor as well as on the duration of exposure (Moberg *et al.* 1999). The detection threshold obtained before and after exposure also shows an adaptation effect that is characteristic of continuous exposure (Haehner *et al.* 2007, Hummel *et al.* 2007). The adaptation and desensitization of the olfactory response were thoroughly reviewed by Kleene (2008).

Some odorants smell qualitatively different at high concentrations. Higher concentrations of any odorant are likely to result in progressively more widespread binding to different types of receptors (Duchamp-Viret *et al.* 1990, Malnic 1999). Rabbit pups responded to the mammary pheromone only when it was presented within a fairly limited concentration range. Only a specific concentration leads to the behavioral response. This is consistent with the notion that higher concentrations actively recruit more receptors, thus

changing the quality of the receptor output (Coureaud *et al.* 2004). It has also been suggested that some olfactory sensitivity differences dependent on sex may exist in humans (Ferdenzi *et al.* 2013), non-human primates (Laska *et al.* 2007a), and dogs (Wells and Hepper 2003). Nucleotide polymorphisms and variations in genes that express olfactory receptors may be the proximate cause of differences between the sexes. Nevertheless, the behavioral relevance (attractiveness or deterrence) of an odorant may be the ultimate cause (Laska *et al.* 2007a). Some gender-based olfactory sensitivity differences were determined with the use of aromatic aldehyde bourgeonal (Olsson and Laska 2010, Ferdenzi *et al.* 2013), but it has also been shown that olfactory thresholds are extremely variable across subjects (Stevens *et al.* 1988) and change substantially over time in humans. This is also the case for shorter periods (Stevens and Dadarwala 1993).

Olfactory receptors in mammals are encoded by the largest gene family charted in the mammalian genome. High number of amino acid changes is affected by high level of polymorphism, high number of pseudogenes and many allelic variants (Quignon *et al.* 2005, Tacher *et al.* 2005). Moreover, the anatomical features of intranasal volumes and the nasal cavity were found to have an influence in dogs (Damm *et al.* 2002). It has been proven that olfactory sensitivity also changes during an animal's lifetime, and this also applies to certain mammalian species (Doty 1989, Wells and Hepper 2003).

It has been suggested that in mammals, such as dogs, that have a very acute sense of smell, an anatomical structure called the olfactory recess determines olfactory superiority in comparison with animals, such humans that lack this structure. It has been demonstrated in the fluid dynamics of canine olfaction that a unique nasal airflow pattern develops during sniffing, which is optimized for odorant transport to the olfactory part of the nose. Thus, mammalian olfactory function and acuity may depend on the transport of odorant molecules to the olfactory recess where the odorant receptors are exposed to prolonged contact with them (Craven *et al.* 2010, Sobel *et al.* 2000). One study, which indicated that apparent sensitivity to some odorants is significantly greater at high nasal flow rates while other odorants exhibit the opposite effect, showed this connection to be contradictory. When the airflow rate and sniffing frequency in mice were evaluated separately, the nasal airflow rate, instead of the sniffing frequency, was found to affect the observed response in the olfactory glomeruli (Oka *et al.* 2009).

In studies conducted on olfactory sensitivity in mammalian species, the experiments focus on the capability of the studied subject to detect the target substance or to distinguish between two or more different substances. In some studies on olfactory sensitivity, the capability to detect a target odorant is considered. The methodology of individual experiments differed in the searching and marking of the target substance as well as in the chemical nature and concentration of the target substance. In recent studies, behavioral tests were used mostly to determine the odor detection threshold. The ODT is determined by testing the animals' ability to discriminate between a target odor and a blind sample that comprises an odorless object. Behavioral tests are based on instrumental conditioning and multiple-choice tests. In multiple-choice tests, the subjects must find and distinctly mark the target substance in different concentrations and are rewarded with food for the correct answer. The descending staircase procedure is usually repeated, and to mix the exact concentration of the target odorant, an odorless solvent is used in the multiple-choice test with a blind sample.

When the concentration detection function is measured, an alternative forced-choice procedure against air as a blank sample and an ascending concentration of target odor are usually used in humans. ODTs were defined as the concentration producing detectability (P) halfway (P=0.5) between chance (P=0.0) and perfect detection (P=1.0). Similar procedures have been used for other mammalian experiments. The odorant concentration is generally indicated in dilute concentration units parts per million (ppm), parts per billion (ppb), and parts per trillion (ppt) and are usually used with vapor phase concentrations. In previous studies, units based on moles or percent were used and generally refer to concentrations in the liquid phase.

Reported olfactory thresholds

Human

Differences in olfactory sensitivity seem to have a genetic basis in humans as well. The olfactory threshold varies greatly across subjects. Olfactory receptors are determined by a large number of olfactory genes that display a high level of polymorphism and nonfunctional pseudogenes (Cometto-Muniz and Abraham 2008). Because human diseases are the main focus of scientific research, the influence of diseases on olfactory sensitivity in humans has been thoroughly explored in subjects with

obsessive compulsive disorder (Browne *et al.* 2006), Parkinson's disease (Harper *et al.* 2005, Haehner *et al.* 2007, Wu *et al.* 2011), diabetes mellitus and its genetic background (Guthoff *et al.* 2009), dementia and Alzheimer disease (Wysocki *et al.* 1997), schizophrenia (Moberg *et al.* 1999), depression (Ferris *et al.* 2007, Croy *et al.* 2014a), and other various dysfunctions. Human emotions (Larsson *et al.* 2000, Brand and Millot 2001, Pause *et al.* 2001, Havlíček 2008) and personality (Havlíček 2012, Pause 2012) may influence olfactory perception and it has been demonstrated that strong negative emotions can reduce olfactory sensitivity (Croy *et al.* 2014a).

In terms of inter-sex differences studies have indicated that women outperform men in specific olfactory threshold measurements (Brand and Millot 2001, Doty and Cameron 2009). Olfactory sensitivity in women may vary within a few days, differences depending on reproductive state (Lundstrom *et al.* 2006) and during the menstrual cycle (Hummel *et al.* 1991, Doty and Cameron 2009) have been found. A review by Martinec Nováková *et al.* (2014) supported the notion that there is a significant cycle-correlated variation of olfactory sensitivity in women (Hummel *et al.* 1991). Olfactory thresholds differed significantly across the cycle; the lowest thresholds were measured during the ovulatory phase and the highest during the menstrual phase (Navarrete-Palacios *et al.* 2003), in a variety of odorants (social and non-social odors), regardless of their different evolutionary significance (Saxton *et al.* 2008, Martinec Nováková *et al.* 2014). These findings support the claim that changes in olfactory sensitivity are linked to a common effect in odor perception in general (Pause *et al.* 2006, Doty and Cameron 2009). Although sexual orientation might play a role in hypothalamus activation in putative hormones (Savic *et al.* 2001, Berglund *et al.* 2006, Savic and Lindstrom 2008), it can be explained by sexual arousal, an acquired sensitization to a specific compound (Berglund *et al.* 2008). It has also been repeatedly proven that olfactory sensitivity decreases with aging (Ezeh *et al.* 1992, Stevens and Dadarwala 1993, Hummel *et al.* 2007, Guthoff *et al.* 2009). According to numerous studies, the repeated introduction of a target odor (even in a perithreshold concentration) causes a decrease in the olfactory threshold and detection sensitivity (Doty *et al.* 1981, Rabin and Cain 1986, Wysocki and Gilbert 1989, Dalton *et al.* 2002, Mainland *et al.* 2002). The brain synapses strengthen with use (Jancke 2009), and everyday olfactory experiences can

improve olfactory performance *via* long-term neuronal plasticity in the olfactory brain regions (Buschhuter *et al.* 2008, Frasnelli *et al.* 2010, Seubert *et al.* 2013). During an investigation in which acetone was used as a target odor, the exposure of experimental subjects to acetone decreased olfactory sensitivity. The ODTs were set at 855 ppm in previously exposed subjects and 41 ppm in non-exposed subjects (Wysocki *et al.* 1997); this was in contrast to increasing sensitivity with experience in investigation cases. This suggests exposure to some substances induces changes in sensitivity, which are specific for this substance (acetone) in particular. The odorant-specific plasticity in the olfactory system is supported by studies that used human steroids as the target odorant. A pronounced decrease in the ODTs of more than four orders of magnitude with repeated exposure was found for the human steroid androstadienone. These experience-dependent changes in threshold were accompanied by a change in perceived odor quality (Lundstrom *et al.* 2003). Androstenedione-anosmic subjects can acquire sensitivity to this steroid hormone by repeated exposure, while subjects who are able to detect androstenedione can lower their threshold with repeated exposure (Jacob *et al.* 2003, Wang *et al.* 2004).

Amyl acetate was used as a target odor when different methods (general procedure, modified constant stimuli procedure, FC-AML procedure, staircase procedure) for determining the ODT were compared. The average threshold of these methods was about 0.11 ppb (Wise *et al.* 2008). In similar studies, certain ODTs were set as low as 0.29 ppb (acetate esters) (Cometto-Muniz *et al.* 2008), 0.14 ppb (aliphatic aldehydes) (Stevens *et al.* 1988), 2 ppm (hydrogen sulfide) and 1.9 ppm (cis-3-hexen-1-ol) (Jaeger *et al.* 2010), which also contain high concentration results such as 500 000 ppm for carbon dioxide or 175 000 ppm for amyl acetate. Specific ODTs for n-alcohols in humans varied from 2.52 ppb (ethanol) to 0.64 ppb (I-octanol) (Cometto-Muniz and Abraham 2008). A subsequent study on humans set the olfactory sensitivity threshold for different organic substances from 245 ppb (ethyl acetate) to 2.9 ppb (hexyl acetate) (Cometto-Muniz *et al.* 2008). Using 2-ketones as the target odorant, the ODT decreased from 832 ppb (acetone) to 5.5 ppb (nonanone) (Cometto-Muniz and Abraham 2009b). For the use of n-alkyl benzenes as a target odor, the specific detection threshold decreased from 89 ppb (octylbenzene) to 2.5 ppb (butylbenzene) (Cometto-Muniz and Abraham 2009a). A similar research study was conducted with aliphatic aldehydes and

helional as the target odors, and the ODTs decreased from 2.0 ppb (propanal) to the lowest threshold of 0.14 ppb (octanal and helional) (Cometto-Muniz and Abraham 2010). The inter-individual threshold variability ranged between one and two orders of magnitude.

The chemesthesis threshold for pungency occurs in concentrations as low as one and as high as six orders of magnitude above the olfactory threshold (Cometto-Muniz and Cain 1990, Cometto-Muniz and Hernandez 1990, Cometto-Muniz and Cain 1991, 1993, 1994). When the effect of aging on olfactory capabilities was examined, butanol was chosen as the target odor, and the olfactory threshold was set at 60 000/l in elderly subjects and at 2200/l in younger subjects (4 % solution v/v of butanol in DHOH (deionized water) corresponding to 3100 ppm in the air) (Stevens and Dadarwala 1993). Female olfactory sensitivity to various alcohols was evaluated as slightly higher than male olfactory sensitivity (Cometto-Muniz and Abraham 2008). For aldehyde bourgeonal, men were able to detect significantly lower concentrations (13 ppb) than were women (26 ppb) (Olsson and Laska 2010), but according to other odor detectability studies, gender was not a significant factor (Stevens *et al.* 1988). In a number of studies, interindividual variability of about one order of magnitude was found between the most and the least sensitive subjects (Cometto-Muniz *et al.* 2008, Cometto-Muniz and Abraham 2009a,b).

Although setting the olfactory detection threshold in humans seems easier than in other mammalian species, the results of olfactory sensitivity studies differ significantly. Thus, the odor detection threshold is a function of the subject's olfactory sensitivity and the experimental method. Attention must be given to the delivery, control, and reliability of the vapor stimulus in measurements of psychometric functions. When the results with the lowest olfactory threshold set are compared, the lowest detected concentration in aliphatic alcohols and aldehydes. The comparison of individual studies is not conclusive because of the methodological differences in olfactometric and psychophysical techniques.

Although the olfactory thresholds are a function of subject sensitivity and method, only a few studies with directly comparable methods used the same subject and stimulus (Wise *et al.* 2008). The current trend is to present olfactory stimuli in the vapor phase (Cometto-Muniz and Abraham 2008, 2010) instead of the liquid phase as in previous behavioral studies (Stevens and

Dadarwala 1993), to obtain the required concentration. The stimulus concentration is most accurate when it is presented in the vapor phase and is calculated from vapor pressures (Cometto-Muniz *et al.* 2003). However, vapor pressure calculated from values taken from the literature may potentially exhibit large differences depending on different literature sources (Stevens and Dadarwala 1993, Cometto-Muniz and Abraham 2010). Therefore, particular computer-controlled vapor delivery devices are currently used to generate and present olfactory stimuli (Cometto-Muniz and Abraham 2008, Cometto-Muniz *et al.* 2008). Gas chromatography quantification of an olfactory stimulus is an indispensable aid today (Cometto-Muniz *et al.* 2008, Cometto-Muniz and Abraham 2009b), but it was not used in earlier studies (Stevens and Dadarwala 1993). The constant stimuli method measures full detection function (Wise *et al.* 2008), while the forced-choice ascending method of limits (Lawless 2010) and the staircase method (Wysocki *et al.* 1997, Linschoten *et al.* 2001, Lotsch *et al.* 2004) provide a reasonable estimate of the average threshold. For individual differences, the constant stimuli method seems to outperform the ascending method (MacMillan 1991) and the staircase method (Linschoten *et al.* 2001, Lotsch *et al.* 2004), which are largely limited (Wise *et al.* 2008).

In the constant stimuli method, the ODT is defined as the halfway point between chance and perfect detection (Cometto-Muniz and Abraham 2008, 2009b), as detectability (detection probability) (Cometto-Muniz and Abraham 2010) or as inverse detectability (Walker *et al.* 2003).

Non-human primates

The sense of smell in primates has been thoroughly examined in comparison to other mammalian species, possibly because primates are closer to humans than any other species. One of the first investigation methods was tested on squirrel monkeys in as early as 1992, and in the following 20 years, various studies focusing on other non-human primate species were conducted (Hudson *et al.* 1992). For olfactory sensitivity, some authors label animals as either "microsmatic" or "macrosmatic"; however, according to some studies (Laska *et al.* 2000b, Smith *et al.* 2004), these terms do not seem to be valid primate descriptors.

An across-species comparison is based on the assumption that New World primates generally are more sensitive than Old World primates. Since the majority of

primate ODT studies were performed in the same laboratory at Linköping University in Sweden, similar olfactometric and psychophysical techniques were used in these studies. The primate subjects were tested using the two-choice instrumental conditioning paradigm (Hubener and Laska 2001, Laska *et al.* 2003). The ODTs were determined by testing the ability to detect a target sample with increasing dilution of an odorant between odorless blank samples. Olfactory stimuli were presented in the gas phase in equimolar concentrations.

One of the first olfactory investigations in pigtailed macaques (*Macaca nemestrina*) determined the specific olfactory threshold for peanut iso-amyl acetate and n-pentanoic acid odors. The animals detected peanut odor in dilutions as low as 1:10 000, and for amyl acetate, the animals detected dilutions from 30 000-fold up to 30 million-fold. The olfactory sensitivity threshold for pentanoic acid ranged between concentrations of 1:30 000 and 1:300 000 (Hubener and Laska 2001).

A study with n-alcohols as target odorants was then carried out in squirrel monkeys (*Saimiri sciureu*) and pigtail macaques (*Macaca nemestrina*). The animals of both species significantly detected concentrations below 1 ppm, and certain individual monkeys even demonstrated thresholds below 10 ppb (Laska and Seibt 2002a). The same methods were used for aliphatic aldehydes (Laska *et al.* 2003), aliphatic esters, and their isomeric forms (Laska and Seibt 2002b). With few exceptions, both species significantly determined concentrations below 1 ppm, and several animals even demonstrated thresholds below 1 ppb (Laska and Seibt 2002b, Laska *et al.* 2003). The detection thresholds for a homologous series of aliphatic esters and isomeric forms were also investigated in spider monkeys. The monkeys significantly detected concentrations below 1 ppm, and in several cases even below 1 ppb (Hernandez Salazar *et al.* 2003). In the case of aliphatic alcohols and aldehydes, the spider monkeys were able to significantly discriminate concentrations below 1 ppm, and certain individual monkeys even demonstrated detection thresholds below 1 ppb (Laska *et al.* 2006b). In accordance with these results, a following comparative study about olfactory detection performance showed a high degree of similarity between the two primate species (squirrel monkeys and pigtail macaques), as well as between these non-human primates and human subjects tested in an earlier study on the same tasks (Laska *et al.* 2005b). Another study

that used acyclic monoterpene alcohols and involved squirrel monkeys, spider monkeys (*Ateles geoffroyi*), and pigtail macaques (*Macaca nemestrina*) showed that squirrel monkeys were significantly more sensitive than the other two species; the squirrel monkeys were able to detect this class of odorants at concentrations below 0.1 ppm (Laska *et al.* 2006a). Nonetheless, a particular comparative investigation performed on substances with apparent behavioral relevance (characteristic of putrefaction processes and fecal odor) in spider monkeys, squirrel monkeys, and pigtail macaques did not show any significant differences among these three primate species. All animals significantly discriminated concentrations below 1 ppm, and in several cases, individual animals even demonstrated thresholds below 1 ppt. The detection thresholds for indol in squirrel monkeys and pigtailed macaques and for ethanethiol in spider monkeys represent the lowest values among more than 50 odorants tested to date. These values are in the same order of magnitude as the lowest detection thresholds that have yet to be reported rats and mice (Laska *et al.* 2007a).

As most of these olfactory studies (Hubener and Laska 2001, Laska and Seibt 2002a,b, Laska *et al.* 2003, 2005a, 2006b, 2007a) were conducted in the same laboratory using the same methods and animals, the threshold values are comparable with great reliability. However, there are some methodological difficulties in between-studies comparison. In two of three non-human primate species, only animals of one sex were available for testing, and the number of subjects was small. A similar methodology complication occurs in dogs studies. In contrast to dog and primate studies, the number of subjects in human and rodent studies is high. A food-reward instrumental conditioning paradigm was used in all non-human primate studies, similar to experiments in dogs and rodents (with the exception of Moulton *et al.* 1960, Krestel *et al.* 1984). Differences in methodology within one laboratory can be seen in the number of choices using the instrumental conditioning. In some studies, there was a two-choice paradigm (Laska *et al.* 2003) while in another study the multiple-choice paradigm was used (Laska *et al.* 2007a). To minimize the possibility of adaptation, between-trial intervals were important as well as the descending staircase concentration procedure (increasing dilutions). When some of the odorant classes were not water soluble, other odorless solvents (diethyl phthalate) had to be used (Laska and Seibt 2002b, Laska *et al.* 2003). In

comparison to the number of human ODTs studies, odorants were presented in the liquid phase without direct conduction to the subjects' faces.

These studies demonstrated that spider monkeys, squirrel monkeys, and pigtailed macaques have a well-developed olfactory sensitivity for different classes of odorants, in comparison to another species classified as microsmatic. A similar methodology allows us to collate experimental results between individual species (Table 1). The results show primates are most sensitive to thiols and indols, while pigtailed macaques were the best-scoring species. In contrast, squirrel monkeys and spider monkeys outperformed when aliphatic alcohols and aldehydes were used as the target odorants.

Across-species ODT comparisons seem to support the contention that comparisons of neuroanatomical features or of the number of functional OR genes are only poor predictors of olfactory performance. The ODT studies emphasize an ecological view that tries to correlate chemosensory performance with the behavioral relevance of the subject odorant (Laska *et al.* 2009, 2010).

Dogs

Dogs are capable of detecting and identifying odorant molecules even in minute concentrations (Quignon *et al.* 2005). The sensitivity of canine olfaction is utilized in many areas, such as biological and abiological scent detection (humans, animals, plants, tobacco, accelerants, bank notes, etc.) (Browne *et al.* 2006). The body of papers that focus on the ability of dogs to detect different types of cancers (Welch 1990, Pickel *et al.* 2004, Willis *et al.* 2004, McCulloch *et al.* 2006, 2012, Horvath *et al.* 2008, 2010, 2013, Cornu *et al.* 2011, Sonoda *et al.* 2011, Bomers *et al.* 2012, Ehmann *et al.* 2012, Bijland *et al.* 2013) as well as diabetes (Dehlinger *et al.* 2013), cirrhosis (Bijland *et al.* 2013), and the first signs of an epileptic seizure (Brown and Strong 2001, Strong *et al.* 2002) is growing. The olfaction of dogs used as a diagnostic tool is often as accurate as, or even superior to, standard diagnostic methods. As our environment is becoming more and more polluted, dogs' sense of smell is useful in pollution and contamination detection (Partyka *et al.* 2014), as well as in mold and other microbial growth detection (Kauhanen *et al.* 2002). Despite technical advances, detection dogs are still a very effective and reliable tool in the search for drugs and explosives (Gazit *et al.* 2003, 2005, Gazit and Terkel 2003, Lorenzo *et al.* 2003,

Browne *et al.* 2006, Singh 2007, Irrazabal *et al.* 2009, Moore *et al.* 2012).

Dogs' ability to respond to concentrations of odorants, which humans cannot normally detect, has been widely exploited and has led to the belief that the sense of smell in dogs is far superior to that in humans. One would expect that the mechanism and sensitivity of canine olfaction have been thoroughly studied, but that is not the case (Moulton *et al.* 1960). Even the canine's legendary sense of smell or the growing reliance on dogs' sense of smell in relation to threats to life and property has not led to a reliable quantification of canine olfactory sensitivity (Walker *et al.* 2006). Despite significant efforts invested in olfaction principles studies, many unanswered questions regarding olfaction and the use of specially trained dogs remain (Harper *et al.* 2005). Although data derived from laboratory studies might be expected to provide reliable information about olfactory sensitivity, published values show differences that are perhaps among the most extreme reported for any sensory perception (Moulton *et al.* 1960). The main complication in using psychophysical methods lies in the differences in detection performance between individual dogs; these differences seem to be related to behavioral variations (Svartberg and Forkman 2002, Adamkiewicz 2013, Jezierski *et al.* 2014), which we can expect in other species, investigated using psychophysical tests.

A study performed by the Canine Behaviour Centre, Queens University, Belfast, showed that dogs are able to determine the direction of a track with the aid of only five individual tracks (Hepper and Wells 2005). This was the only study to date that has reported differences in olfactory sensitivity between male and female domestic dogs. Male dogs identified the correct direction of a given track more frequently than did female dogs, and younger dogs performed better than older animals (Wells and Hepper 2003). The same research team also confirmed pre- and post-natal learning regarding chemosensory stimuli in puppies (Hepper and Wells 2006). Gender-specific induction of enhanced sensitivity was found in male dogs which generally outperformed female dogs. These findings are contrary to olfactory studies in humans; studies indicate women outperform men with specific odorant substances, such as sex hormones (Brand and Millot 2001, Doty and Cameron 2009). Regardless, no reliable sex differences have been found in dogs (Wells and Hepper 2003) or in humans (Olsson and Laska 2010, Ferdenzi *et al.* 2013).

Table 1. Olfactory detection thresholds for laboratory chemical substances in vapor phase in ppm concentration.

Chemical class	Chemical substance	Human	Pigtail macaque	Spider monkey	Squirrel monkey	Dog	Mouse
<i>Aliphatic alcohols</i>	pentanol	x	0.29	0.0004	0.0004	x	0.00003
	hexanol	x	0.006	0.006	0.006	x	0.0003
	heptanol	x	0.0032	0.0003	0.00031	x	
	octanol	0.00064	0.0048	0.0048	0.048	x	
	propanal	0.002	x	x	x	x	
<i>Aliphatic aldehydes</i>	butanal	x	0.0004	0.039	0.0039	0.00004	
	pentanal	x	0.148	0.00148	0.0148	x	
	heptanal	x	0.0024	0.00235	0.00235	0.00004	
	hexanal	0.00014	0.00052	0.0052	0.052	x	
	ocatanal	0.0014	0.0016	0.00016	0.16	x	
<i>Acetate esters</i>	burgeonal	x	x	x	x	0.000000001	x
	amyl acetate	0.00011	0.14	x	x	0.0000114	
	ethyl acetate	0.245	x	0.036	x	x	0.0000041
	butyl acetate	0.0043	x	0.00006	x	x	
	pentyl acetate	x	x	0.000027	x	x	
	hexyl acetate	0.0029	x	0.00013	x	x	
<i>Carboxylic acids</i>	butanoic acid	x	x	x	x	x	0.000003
	pentanoic acid	x	x	x	x	x	0.000003
<i>Amid acids</i>	panthotenic acid	x	0.0019	x	x	x	x
<i>Nitroalkanes</i>	dimethyl dinitrobut.	x	x	x	x	0.0005	x
<i>Thiols</i>	ethanethiol	x	0.000096	0.0000096		x	x
	butanethiol	x	0.000016	0.00016	0.00016	x	x
	pentanethiol	x	0.00063	0.00063	0.00063	x	x
<i>Thiazolines</i>	trimethylthiazoline	x	x	x		x	40.00
<i>Indols</i>	indole	x	0.00000003	0.0003	0.00000003	x	x
	methyl indole	x	0.000037	0.0000037	0.000012	x	x
<i>Ketones</i>	nonanone	0.0055	x	x	x	x	x
<i>Sulfides</i>	hydrogen sulfide	2.00	x	x	x	x	x
<i>Amino acids</i>	cystein	x	x	0.0013	x	0.0000044	x
	methionine	x	x	0.0011	x	0.000036	x
	proline	x	x	0.002	x	0.023	x
<i>Alkylpyrazines</i>	pyrazine	x	x	27.80	x	0.028	x
	methyl pyrazine	x	x	0.044	x	0.0001	x
	tetramethyl pyr.	x	x	0.00063	x	0.00000092	x
	butylbenzene	0.00025	x	x	x	x	x
<i>Benzenes</i>	octylbenzene	0.00029	x	x	x	x	x
	propylthietane	0.0000000059	x	x	x	x	x
	methylbutyl form.	0.0000000013	x	x	x	x	x
<i>Sulfur-containing volatiles</i>	propylthiethane		x	0.0000074	x	0.00003	x
	butanethiol	0.00000052	x	0.0000026	x	0.00000003	x
	phenylethyl sulfide	0.0000016	x	0.0000012	x	0.00000003	x
	methylbutyl form.		x	0.0000052	x	0.000003	x
<i>Oxides</i>	carbon dioxide	x	x	x	x	x	700.00

Olfactory sensitivity may also differ between dog breeds. When the additional olfactory receptor gene polymorphism was identified in 20 various breeds, some mutations were found to be breed-specific (Quignon *et al.* 2005, Tacher *et al.* 2005). No study has been published that compared the olfactory thresholds of various dog breeds. A recent study that compared the olfactory performance of Pugs, German Shepherds, and Greyhounds did not determine their ODT either; nevertheless, in an experiment in which the dogs were supposed to alert to various dilutions of the target odor, Pugs significantly outperformed German Shepherds while Greyhounds could not be tested because of a lack of motivation (Hall *et al.* 2015).

The first investigations dealing with canine olfactory sensitivity compared humans and dogs. According to the earliest studies, olfaction sensitivity in dogs is much better than that of humans (Neuhaus 1953, Laska *et al.* 2008a). The next two investigations revealed that the olfaction sensitivity in canines was approximately the same as that in humans (Nicollini 1954, Becker 1962). A later study found that the olfaction sensitivity in dogs was approximately 100 times greater than that in humans (Moulton *et al.* 1960). However, the previously mentioned publications (Neuhaus 1953, Ashton 1957, Moulton *et al.* 1960, Krestel *et al.* 1984) do not provide data that may be relied upon with confidence (Walker *et al.* 2006).

One of the first studies on the olfactory threshold in dogs was conducted by Neuhaus (1953) and compared dogs and humans. The olfactory threshold in dogs for butyric acid and acetic acid was 8 log units below that in humans. Another study, which compared specific olfactory thresholds in dogs and humans, was conducted by Kaise (1969). The olfactory threshold in dogs for clove oil was estimated at approximately 6 log units below that in humans (Laska *et al.* 2008a). The canine ability to detect n-aliphatic acids was investigated by Ashton *et al.* (1957). The results showed individual differences in two dogs. Performance also varied with the target substances depending on the number of carbon atoms in the molecules of both acid groups. The detectable concentrations were approximately 1.54-0.801 log units of molar concentration.

The results of other studies (Nicollini 1954, Becker 1962) performed on dogs differed considerably. Canine and human olfaction sensitivity was compared again, and the results showed that dogs and humans had the same level of olfaction sensitivity. Three years later,

Moulton *et al.* (1960) noted canine olfaction sensitivity was 2 log units below that of humans. The study was carried out with only two Labrador hybrids, and a specific olfactory threshold was determined for fatty acids. The results showed significant differences between the two dogs tested but also between the sensitivity of the two fatty acid groups. A later study by Marshall and Moulton (1981) reported similar results. The canine olfaction threshold was found to be 2-4 log units below that of humans. Krestel *et al.* (1984) also conducted a study focused on the comparison of olfaction in dogs and humans, but the results determined a specific threshold for amyl acetate. The dogs were trained to put their heads into a wooden box, into which the odorant was released. The dogs (six Beagles) were motivated and rewarded with water (deprivation by thirst) and punished with an electrical shock. The results presented a specific canine olfactory threshold 2.6 log units lower than that of humans.

About 20 years later, Pickel *et al.* (2004) studied a specific olfactory canine threshold for amyl acetate while dealing with disease diagnostics. He observed surprising values, and the olfactory threshold was set to a concentration of about 1-2 ppt. The next study investigating olfactory sensitivity in dogs was conducted by Walker *et al.* (2006). The target odorant was the same substance that was used by Krestel *et al.* (1984), i.e. amyl acetate. In a relatively small sample of only two dogs (a Schnauzer and a Rottweiler), they found remarkable values (1.9 and 1.14 ppt) that were roughly 30 to 20 000 times lower than the range of thresholds reported in previous studies (Krestel *et al.* 1984). Walker *et al.* (2006) believed their method “find the target”, which is based on positive conditioning and includes more natural and non-restrictive conditions outside the laboratory, is the main cause of the difference between their study and studies that use “more conventional methods”. These results indicate that canine olfactory sensitivity may be much higher than previously thought (Walker *et al.* 2006).

Dogs that received steroids exhibited a significant elevation in their detection threshold for benzaldehyde and eugenol, and thus it seems that olfactory acuity could also be influenced by hormones (Ezeh *et al.* 1992).

Studies dealing with canine sensitivity in detecting explosive substances are very rarely published. One of the few studies conducted by the Institute for Biological Detection Systems at Auburn University

identified the specific olfactory thresholds for methyl benzoate, cyclohexanone, and nitroglycerin as ranging from ppb to ppt units (Johnston 1999). Laboratory workers from the Bureau of Alcohol, Tobacco and Firearms found that dogs were able to respond to nitromethane diluted in water in concentrations of one to one trillion. However, much lower concentrations were also mentioned in this study (Kury and Strobel 2003). Adequate olfactometry and behavioral control is often lacking in canine olfactory sensitivity studies. However, differences in the design methodologies of canine olfactory sensitivity studies may produce inaccurate comparisons (Johnston 1999).

The results of ODT studies are essentially incomparable. A small number of olfactory sensitivity experiments in dogs were conducted over a long period, and the olfactometric and psychophysical techniques differed substantially. Single experiments focused on different target odorants, and various dog breeds were used as experimental subjects. Unequal behavioral testing was applied, and the preparation of the odorant sample differed across studies, as well as odorant dilution devices. Moreover, the results were often published as a comparison with humans and described only the difference, without a specific concentration. In general, ODTs in dogs were distinctly the lowest when amyl acetate was used as a target odorant (Walker *et al.* 2006) although the author himself admits the possibility that it is caused by their new methodology.

Similar to other ODT psychophysical experiments, most substantial between-studies differences are found in olfactometer design and test procedure. Descending concentration testing can enhance the absorption effect and provoke olfactory adaptation, so ascending concentration testing is usually preferred (Gostelow *et al.* 2001). As in non-human primate psychophysical experiments, dog experiments are based on operation conditioning; however, in contrast with olfactory studies in primates, the odorant dilution devices differ (Shepherd 2004, Craven *et al.* 2010). A substantial difference in methodologies can be found even between experimental designs of canine studies and huge differences in results in ODT concentrations spring there. According to the latest experimental approaches, the absence of any deprivation during training (physical pain, lack of water or food), as well as the method of target odorant detection (stationary odorant chambers or active finding of the target), causes differences in orders of units (Walker *et al.* 2006, Craven *et al.* 2009). Ascending

staircase (decreasing dilution) of odorant concentration is always used in canine experiments, as well as in primates, but the emphasis is placed on the piecemeal descending staircase (increasing dilution) of the concentration to avoid olfactory adaptation by the subjects (Walker *et al.* 2006).

Rodents

Rats (*Rattus rattus*) have a highly developed ability to detect and identify odorants in minimal concentrations (Quignon *et al.* 2005). Although, to date, sniffer dogs remain a still indispensable and very effective means of explosive detection (Moore *et al.* 2012), African giant pouched rats (*Cricetomys gambianus*) have been trained to detect buried landmines (Corcelli *et al.* 2010, Poling *et al.* 2011) and are able to detect tuberculosis (Mahoney *et al.* 2012, Mgone *et al.* 2012). One of the basic factors influencing olfactory acuity is the animal's feeding state. According to a study by Aime *et al.* (2007), food-deprived rats exhibited increased detection at low concentrations, which led to the conclusion that olfactory sensitivity increases in food-deprived animals (Aime *et al.* 2007). Olfactory performance improves with repeated exposure to a particular substance in other mammalian species as well as in rats (Doty and Ferguson-Segall 1989, Wilson 2000, Wilson and Stevenson 2003) and mice (Wang *et al.* 1993, Yee and Wysocki 2001). One of the first olfactory sensitivity studies performed in mice (*Mus musculus*) focused on the absolute detection threshold for ethyl acetate, which was set below 0.41 ppt. When the same methods are used, this value is similar to that obtained in rats (*Rattus rattus*) (Dalton *et al.* 2002). Laska *et al.* (2007b) investigated the ability of discrimination between odorant pairs, first with homologous series of aliphatic aldehydes. The animals were able to discriminate between two odorant pairs when the stimuli were presented at concentrations of 1.00, 0.01, and 0.001 ppm, and mice also have an excellent ability to discriminate between structurally related aliphatic odorants. The mice were also able to distinguish between 50 stimuli that were presented at a gas phase concentration of 1 ppm. The same laboratory later examined the ODTs, and aromatic aldehydes were used as the first target odorants. When all seven stimuli were considered, the mice detected concentrations as low as 0.01 ppm from the solvent, and with bourgeonal, the animals detected concentrations as low as 0.1 parts per quadrillion, which constitutes the lowest olfactory detection threshold value reported in this

species to date (Larsson and Laska 2011).

In a subsequent study, eight structurally related aliphatic C-6 alcohols and aldehydes were used as the target odorant, and all mice detected concentrations below 0.03 ppm. With three of the substances, the best-scoring animals were even able to detect concentrations below 0.03 ppb (Laska *et al.* 2008a). Further comparisons suggest that odor structure-activity relationships are substance class-specific and species-specific (Can Guven and Laska 2012).

ODT studies in rats have also presented results as volume percentages, which make it difficult to compare these studies with previous studies. The detection threshold for CO₂ was estimated at about 700 ppm (Ferris *et al.* 2007).

When microsmatic and macrosmatic mammalian species were compared, mice or rats were used as the subject organism several times in the psychophysical laboratory of Linköping University in Sweden, which make the results at least partially comparable (Table 1). The same methodological principles were a significant advantage in rodent experiments (almost exclusively in mice), similar methodologies found in non-human primates, but lacking in other mammalian ODT studies. The same methodological rules were followed by using automated liquid-dilution olfactometer, near-odorless diethyl phthalate as a solvent, the instrumental conditioning procedure, and the increasing dilution of the target odorant. An important point is the choice of experimental subjects: an outbred strain of mice was used for the experiments as the mice's genetic background is more similar to wild-type mice than that of inbred strains (Laska *et al.* 2007b, Laska *et al.* 2008a, Larsson and Laska 2011, Can Guven and Laska 2012). In rats, target odorants were chosen to investigate the behavioral context, and the results suggested the behavioral relevance of an odorant plays an important role as a determinant of a species' olfactory sensitivity. The across-species experiments in mice allow us to compare the ODT concentrations with some other mammalian species, primarily non-human primates. In general, mice are more sensitive to alkyl pyrazines, amino acids, and aliphatic esters and to aliphatic aldehydes, where the lowest ODT values were reported in this species thus far. Mice were able to detect smaller concentrations than non-human primates when six sulfur-containing volatiles known as components of the odors of natural predators of the mouse were used. When aliphatic alcohols are used, the ODTs in mice are equal to ODTs in humans and non-

human primates.

Other mammalian species

In other mammalian species, olfactory sensitivity research is lacking substantially and is mostly confined to studies focused on a number of olfactory cues the subject can easily distinguish. Studies have investigated the South African fur seal (*Arctocephalus pusillus*) (Laska *et al.* 2008b, Laska *et al.* 2010), the Asian elephant (*Elephas maximus*) (Arvidsson *et al.* 2012), and the short-nosed fruit bat (*Cynopterus sphinx*) (Ganesh *et al.* 2010, Zhang *et al.* 2013). Studies dealing with olfactory detection thresholds in other mammalian species are very rare. The only study of greater significance was carried out using Göttingen minipigs (*Sus scrofa domestica*). The ODTs for ethyl acetate and ethanol were determined as a concentration as low as 5 ppm (Sondergaard *et al.* 2010), which is far from the lowest ODT reported in other mammalian species, but it is important to point out the inconsistencies in methodology. As experiments in these species are still in their infancy, they are focused on the ability of determination, in contrast with olfactory threshold experiments in primates, dogs, or rodents. Therefore, a between-species olfactory sensitivity comparison based on these studies is not possible.

Between species comparison

The quantitative structure-activity relationship (QSAR) is clearly described by Cometto-Muniz and Abraham (2008, 2009a,b, 2010) and Cometto-Muniz *et al.* (2008) and a significant positive correlation between ODTs and carbon chain length was found in other mammalian species (Laska and Teubner 1998, Laska *et al.* 2000a, 2008a, Laska and Hubener 2001, Laska 2005, Arvidsson *et al.* 2012, Can Guven and Laska 2012). In an inter-species comparison study that used six sulfur-containing components of odors of natural mice predators, 12 subjects were able to detect concentrations below 0.01 ppm; when four of these odorants were used, the best-scoring subjects were able to detect even concentrations below 10 ppt. In this study, the mice were more sensitive to the tested odorants, and olfactory sensitivity did not differ substantially among the human subjects.

The evidence of a low specific olfactory threshold in squirrel monkeys and humans for carboxylic acids was provided and supports the assumption that human and non-human primates may share common

principles of odor quality perception (Laska and Teubner 1998). Another investigation that compared non-human primates and rodents was performed with substances with apparent behavioral relevance (characteristic of putrefaction processes and fecal odor) in spider monkeys, squirrel monkeys, and pigtail macaques. No significant differences between these three primate species were found. All animals significantly discriminated concentrations below 1 ppm, and in several cases, individual animals even demonstrated thresholds below 1 ppt. The ODTs for indol in squirrel monkeys and pigtailed macaques and for ethanethiol in spider monkeys represent the lowest values among more than 50 odorants tested to date. These values are in the same order of magnitude as the lowest detection thresholds that have yet to be reported in rats and mice (Laska *et al.* 2007a). Next, a study testing primates and mice was conducted with three female spider monkeys. They were able to detect aliphatic alcohols and aldehydes at concentrations below 1 ppm, and six of the eight stimuli were detected at concentrations below 0.1 ppm by the animals with the highest olfactory sensitivity. Mice even outperformed non-human primates with ODTs for aliphatic alcohols below 0.01 ppm (Lotvedt *et al.* 2012).

The behavioral relevance of trimethylthiazoline (a volatile component of the anal gland secretion of the red fox) was the main issue of between-species comparison between rats and three primate species. The three primate species, which are all non-prey species of the red fox, were able to detect concentrations in ppb units, which do not rank among the lowest olfactory thresholds reported for these species. Rats, a natural prey species of the red fox, were able to discriminate concentrations between 0.04 and 0.10 ppt, which is by far the lowest olfactory detection threshold for an odorant reported in rats to date (Laska *et al.* 2005a).

Olfactory sensitivity for alkyl pyrazines in mice and spider monkeys was tested in a comparative study (Laska *et al.* 2009). The spider monkeys were able to detect five stimuli at concentrations below 1 ppm, and with one stimulus, they were able to identify concentrations even below 1 ppb. With all six alkyl pyrazine stimuli, mice were able to detect concentrations below or equal to 0.1 ppm, with the best-scoring individuals detecting concentrations below or equal to 0.1 ppb; these results indicate that mice may be more sensitive than spider monkeys. Another comparison of the detection thresholds between mice and spider monkeys was performed for three amino acids. The best-

performing spider monkeys detected concentrations below 1 ppb. All the mice detected concentrations equal to or below 0.1 ppm, and the best-scoring animals were able to detect concentrations even below 0.1 ppb (Wallen *et al.* 2012). The results of these two studies indicated that mice were more sensitive than spider monkeys. In an additional comparison study that included humans, spider monkeys, and mice, six sulfur-containing components of the odors of natural predators of mice were used as target odors. The spider monkeys were able to detect concentrations below 0.01 ppm, and four of these odorants were detected at concentrations below 10 ppt by the animals with the highest olfactory sensitivity. In this study, the mice proved to be more sensitive to the experimental odorants; however, the human subjects did not differ significantly.

When olfactory detection thresholds for seven aromatic aldehydes were determined, no general differences between olfactory sensitivity in humans and that of spider monkeys were observed (Kjeldmand *et al.* 2011). Both species detected concentrations lower than 1 ppm for all odorants, and certain individuals even distinguished concentrations lower than 1 ppb for several odorants.

These results support the assumption that the behavioral relevance of an odorant may be an important determinant of a particular species' olfactory sensitivity. In the future, it might be useful to select target substances used in ODT comparisons by their behavioral relevance to each of the investigated species.

Conclusions

As a result of intensive research activities in physiology, genetics, anatomy, and behavior, knowledge surrounding the mechanisms underlying olfactory perception has increased significantly within the last two decades. Nevertheless, many questions remain open despite the immense progress made. Among these questions are those that deal with olfactory thresholds and olfactory system sensitivity. Physiological principles that determine a specific olfactory sensitivity are still unclear, and after several papers that deal with the behavioral testing of various mammalian species were reviewed, it is still not possible to conclude which anatomical or physiological characteristics are responsible for higher or lower thresholds to specific substances.

An overview of olfactory sensitivity in most studied mammalian species is presented here, together

with basics of olfactory perception and olfactory sensitivity factors. The results of the more than 40 studies presented provide further evidence of low specific olfactory thresholds in mammalian species. These research findings lend further support to the suggestion that genetic or neuroanatomical between-species comparison cannot be taken as a reliable predictor of olfactory performance.

According to the current research developments, scientific attention is increasingly focused on how olfactory sensitivity changes are associated with diagnosis of human diseases (Wu *et al.* 2011, Guthoff *et al.* 2009, Moberg *et al.* 1999, Croy *et al.* 2014b). The rise of this field of study is closely related to the development of high-resolution magnetic resonance (Welge-Lussen *et al.* 2009, Toledano *et al.* 2012, Croy *et al.* 2014c) and event-related potentials recording (Kayser *et al.* 2011). Another rapidly developing research area is closely linked to the between-species comparisons described in this review, and investigations focused on olfactory gene expression (Quignon *et al.* 2005, Tacher *et al.* 2005) not only in mammals (Laberge and Hara 2004).

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As is made clear in this article, no studies have demonstrated a direct connection between olfactory sensitivity and an absolute number of specific olfactory receptors, the density of ORs in the olfactory epithelium, or the size and quality of the olfactory structures in the brain. An ecological view of olfactory sensitivity correlated with the behavioral relevance of odor stimuli offers a future approach in the significance of olfaction in mammalian species. The detectability of odorants may also be affected by their behavioral relevance and frequency of occurrence in the environment of the receiving subject. Future behavioral research in the field of specific olfactory sensitivity should focus on differences associated with species, breeds, sex, previous exposure, and behavioral relevance. A uniform comparable methodology of etho-physiological experiments has not been introduced. In the future, more integration of component studies should be followed, leading to a uniform methodological approach.

Conflict of Interest

There is no conflict of interest.

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10 CONCLUSIONS AND PERSPECTIVES

Multimodal communication is essential in social interactions in fish, including conspecific recognition and agonistic interactions. Behavioral experiments have shown that fishes are unlikely to respond to agonistic sound stimuli alone (Blais et al., 2009; Raffinger and Ladich, 2009), but adding visual stimuli to acoustic stimuli increases behavioral response in agonistic encounters (Valinski and Rigley, 1981; Bertucci et al., 2010; Estramil et al., 2014). In courting behavior behavioral response increase when adding acoustic signals to visual signals. Female cichlids favor males using vocal and visual cues over males using only visual displays (Maruska et al., 2012). Courtship sound accompanies a specific behavior to more clearly denote the intentions of the signaler (Amorim et al., 2013). Only a few studies however focus on how signals of different modalities interact to elicit appropriate behavioral answer (Smith and Evans, 2013). The role of particular senses in particular behavior and the relative hierarchy of sensory systems in providing input in behavior remain unclear. More studies are needed to determine how much different sensory channels participate on multimodal communication, and the hierarchy of modalities (Hebets, 2011).

Computer manipulated image stimuli and sound playback offer powerful tools to assess the relative relevance of single modalities and it represent an approach of increasing importance. However methodological and technical procedures need to be prepared with great caution. The major aim of usability research of computer manipulated stimuli is to formulate consensual methodological approach for different animal species confirmed by independent behavioral studies. There are many ways to improve computer animation and video playback as reviewed above. If designed carefully, this approach can be used to address an almost unlimited range of questions. As soon as the computer manipulated stimuli are reliably perceived, next step may be to change single traits of the stimuli.

The aim of the study Computer manipulated stimuli as a research tool in Mozambique tilapia *Oreochromis mossambicus* (Wackermannová et al., 2017) was to investigate whether this fish species responds to computer manipulated visual stimuli and acoustic playback. Six experiments were conducted combining visual computer manipulated stimuli, live stimuli and a mirror with acoustical computer manipulated stimuli, white noise or no sound. Our results suggest that non-interactive computer manipulated visual stimuli as not a suitable tool in

behavioral research in Mozambique tilapia *O. mossambicus*. However, use of acoustic computer manipulated playbacks increase its reactivity to live stimuli. Live stimuli and acoustic computer manipulated playbacks of conspecific sounds are relevant tools for behavioral studies, whereas visual computer manipulated stimuli do not elicit significant behavioral reaction. Nonetheless, further multimodal signaling studies in Mozambique tilapia *O. mossambicus* are required, as multimodality is an important aspect and using artificial stimuli combination of different sensory modalities might disentangle multimodal communication in fish (Wackermannová et al., 2017).

When animals compete about resources a number of intrinsic and extrinsic factors interacts together to determine contest outcome. Competitive abilities and behavioral strategies of animals can also be expressed as changes in movement activity (Brodin, 2008). Animals show decreased activity in presence of dominant conspecifics (Wolf et al., 2007). Intruders are expected to be more active, as these individuals are bolder and more aggressive (Cote et al., 2010). Effects of social (familiarity, *Residency effect*) and environmental factors and individual characteristics (body size) as competition predictors were examined in the study Familiarity, prior residency, resource availability and body mass as predictors for the movement activity of the European catfish (Slavík et al., 2016a). Body size, resource availability, familiarity and *Residency effect* decrease moving activity in European catfish *S. glanis*. When an individual is substantially large its movement activity decrease to minimum irrespective of factors including familiarity and *Residency effect*. In an encounter of large and small individual, moving activity is lower in large individuals (high *RHP* individuals). Considering moving activity as a stress indicator, it can be concluded that *Residency effect* and higher *RHP* reduce stress of limited resources (Slavík et al., 2016a). The smaller an individual was relative to the mean body mass, the higher the influence of familiarity and prior residency. This is consistent with *Value asymmetry hypothesis* (Dill, 1983) and *Pay-off asymmetry hypothesis* (Enquist and Leimar, 1987) predicting resource holder to win as *Resource value* increases over time. Residents defend their territories when using advantage of prior residency and higher motivation to defend valuable resources. How particular competition factors - *Resource value*, *RHP*, *Winner-looser effect*, *Residency effect* or *Dear enemy effect*, which are supported by theoretical hypotheses – *RHP*-, *Value asymmetry*-, *Pay off asymmetry*-, interact together is the subject of further interest in competition studies.

Coloration is an important communication channel in fish (O'Connor et al., 1999). Color changes indicate dominance, decrease agonistic interactions and stabilize dominance hierarchy among conspecific (Volpato et al., 2003). Physiological and behavioral differences

in albino individuals result in loss of schooling behavior (Kowalko et al., 2013) and in loss of hierarchy dominance and aggressiveness (Elipot et al., 2013). Albino catfish *S. glanis* tend to be spatially separated from a group of pigmented conspecifics (Slavík et al., 2015). Agonistic behavior in albino and pigmented conspecifics was studied in study the How does agonistic behavior differ in albino and pigmented fish (Slavík et al., 2016b). Level of aggression is lower in albino than pigmented European catfish *S. glanis*. Albino juveniles are less aggressive compared to their pigmented conspecifics. They also show higher tendency to separate spatially than pigmented individuals that show tendency towards closer contact. In conclusion albinism is associated with lower aggression, lower dominance and social exclusion (Slavík et al., 2016b). How some fish species non-visual fish species, such as European catfish determine *RHP* or color of their conspecifics is not studied yet. To investigate relative *RHP* in audio playback, recordings of different sized individuals can be played back, also combined with olfactory stimuli in non-visual species such as European catfish *S. glanis*.

The omnipresent chemical stimuli enable detection and discrimination of home range, conspecifics, mates, food resources and predators. Olfactory sensitivity is a crucial communication channel, but still not well-studied. Reviewing more than 40 olfactory sensitivity studies, it can be concluded that genetic or neuroanatomical between-species comparison cannot be taken as a reliable predictor of olfactory performance (Wackermannová et al., 2016). Specific physiological properties are a basic insight needed for a successfully conducted behavioral experiment. However, scientists depend in most cases on behavioral testing. Recently, the number of olfaction studies in fish is increasing in relation to multimodal communication (Thunken et al., 2014; Keller-Costa et al., 2015). Olfactory cues play an important role in dominance signaling (Oliveira et al., 1996; Almeida et al., 2005) and further research in olfaction in competitive encounters is expected. An open direction may be studying reaction of territorial males toward urine of other territorial males with different *RHP*.

Based on the results, many further directions of investigation ensue. Questions about how single modalities contribute to final perception in agonistic behavior of different fish species remain unclear. Coming out of angle of view of man, it is natural to emphasize investigation of visual communication. However, if we consider physiological properties and environmental conditions of Mozambique tilapia *O. mossambicus* and European catfish *S. glanis*, this leads us to investigation of other senses such as hearing and olfaction (Bruton and Bolt, 1975; Alp et al., 2004). Not only night active European catfish *S. glanis*, living at

muddy bottoms, but also shallow water Mozambique tilapia *O. mossambicus* were shown to rely on other communication channels than visual (Oliveira et al., 1996; Pohlmann et al., 2001). Combining, for example, visual signals (playback, live fish) with acoustic (playback) olfactory signals (territorial male urine) may help in uncovering relative importance of single modalities in fish. Subsequent modification of used stimuli (using displays, sounds or urine of different *RHP* males) may than provide an insight into competitive factors. Changing colors of played back object fish by computer manipulation may show how pale or bright coloration influences agonistic response in territorial male. Computer manipulated stimuli are useful tool for conducting behavioral studies focused on communication and competition in fish. Nevertheless, suitability for single species has to be verified as there pronounced interspecific differences in signal perception. A whole range of technical and methodological constrains may occur as well. Although our studies emphasize methodological examination and further rigor in design of visual and acoustic playback stimuli, utilization of computer manipulated stimuli in behavioral studies is encouraged.

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