DETERMINANTS OF DECISION MAKING IN CLIMBING PERCH (*Anabas testudineus* BLOCH), A FRESHWATER FISH

By

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Kerala, India.

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Declaration

I, V. V. Binoy do here by declare that this thesis entitled **Determinants of Decision Making in Climbing Perch *(Anabas testudineus* Bloch)**, **a Freshwater Fish,** is a genuine record of research works done by **me** under the guidance of Dr. John Thomas K., Reader, Animal Behaviour and Wetland Research Laboratory, Research and Post Graduate Department of Zoology, Christ College, Irinjalakuda in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Zoology of The University of Calicut.

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This is to certify that this thesis entitled **Determinants of Decision Making in Climbing Perch *(Anabas testudineus* Bloch), a Freshwater Fish**' is an authentic record of the research works carried out by **Mr. V. V. Binoy** under my supervision and guidance in partial fulfilment of the requirement of the degree for Doctor of Philosophy in Zoology of the University of Calicut.

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This is to certify that **Mr. V. V. Binoy** has completed the research work for the full period prescribed under the Ph.D. ordinance of the University of Calicut. This thesis entitled '**Determinants of Decision Making in Climbing Perch *(Anabas testudineus* Bloch)'** embodies the results of his investigation conducted during the period at which he worked as a research scholar. I recommend the thesis to be submitted for evaluation for the award of the degree of Doctor of Philosophy in Zoology of the University of Calicut.

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Principal

Dedicated to…….

All animals sacrificed for the successful completion of my education and experiments. All kind hearts dreamed and prayed for my success in the field of science.

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Preface

The processes and functions of decision making in animals are highly discussed and fast growing areas of contemporary scientific research. This subject has attracted the attention of scientist working in various disciplines, like psychology, neuroscience, ecology, conservation, cognitive science, zoology and thus an interdisciplinary approach has been followed all over the world to understand the basis of this phenomena. A detailed knowledge of decision making ability of animals is essential for understanding the evolution of decision making, and has several applications in the field of conservation biology. Fishes are excellent model system to study various aspects of decision making and many scientists consider them equivalent to primates in handling complex decision making situations. In India studies dealing with animal decision making are scanty and studies on decision making in fish are totally absent in Indian science literature.

The present thesis deals with various aspects of fish decision making, using climbing perch (*Anabas testudineus* Bloch*)* model system. In section I, the influence of familiarity (with conspecifics as well as with heterospecifics), the key factor of social cohesion, on decision making in various sociobiologically significant contexts are discussed. Here, binary choice was the assays used for the evaluation of decision making.

Section II of the thesis deals with the propensity of climbing perch to take risky decisions (boldness), using the latency to initiate the exploration of a novel area as the assay. Here, the influence of biologically significant factors like, presence of conspecific and/or predator, and habitat quality on the ability of climbing perch, in taking a risky decision is analyzed. Additionally, the development of boldness in fish reared in homogenous habitat is compared with the fish collected from natural habitat.

Following the conventions of fish biologists the term fish is used for denoting the focal species climbing perch, no matter whether it is singular or plural, through out the thesis. Similarly the term fishes refer to different species of fishes or the class Pisces in general.

The investigations started in December 2001 and completed in December 2008. The studies were carried out in Animal Behaviour and Wetlands Research Laboratory, Department of Zoology, a recognized research centre of the University of Calicut under the supervision of Dr. John Thomas K.

DETERMINANTS OF DECISION MAKING IN CLIMBING PERCH *(ANABAS TESTUDINEUS* BLOCH), A FRESHWATER FISH

ABSTRACT

The ability of climbing perch (*Anabas testudineus*, Bloch,) to take a decision in conflicting situation and the influence of external and internal factors on the decision making ability was analysed using behavioural assays: shoal selection and the propensity to take a risky decision.

The results reveal that familiarity, the focal internal factor, has a determining role in the decision making ability of this species. Normally, this fish prefer larger shoal to smaller shoal. However, they can acquire familiarity with conspecifics and heterospecifics, and the familiarity thus developed can bias the shoaling decision. Climbing perch recognizes and prefers familiar conspecifics and heterospecifics to shoal with. The acquisition of familiarity with conspecific is depended on visual characteristics of the stimulus fish and only the heterospecifics with a shape similar to that of conspecific was able to induce familiarity based decision bias in this species

The propensity to take a risky decision (boldness) in climbing perch was found to be consistent in different situations. Development from the egg stage to adult in a homogenous habitat failed to influence the boldness of this species. Biologically significant fear evoking factors like predator, aquatic and aerial predators, predator odour, skin extract of conspecific, failed to affect the boldness of climbing perch. However, a microhabitat with a substratum composed of cobbles and the presence of an eyespot were found to inhibit the climbing perch from taking risky decisions.

Contents

DECISION MAKING IN ANIMALS

All animals face a variety of conflicting situations in everyday life. Conflicting situations can occur when several different events or targets appear coincidently. For example, when a prey and a predator appear simultaneously before a hungry animal, it may have to take a decision either to approach the prey or to flee from the predator. In the context of reproductive behaviours, a sexually mature male may be in conflict to take a decision when approaching its mate while defending against intruder males (cf. Satou *et al.* 1984). Conflict might occur even for a single behaviour. To illustrate, a foraging animal is confronted with a choice of two food targets with different features or values such as high food density near the predator versus low food density without any risk. In such a conflicting situation the decision making comes to rescue the animal from the inconsistency.

Earlier it was believed that animals simply respond to stimulus without having any comprehension about the consequences of its response (Chandroo *et al.* 2004). According to Premack (2007) animals have several abilities, once thought unique to the human beings. Recent studies show that animals possess the ability to give selective attention to internal and external stimuli, anticipation, and expectation and to make complex decisions involving higher level cognitive processing (Heyes, 1993; Dickinson and Ballein, 1994). All these studies point that decision and decision making is not restricted to *Homo sapience* and but also seen in organisms with a simple nervous system to animals with very complex brain and neural circuitry (Zhang, *et al.* 2005; Bateson, 2004). Animals choose mates (Bateson, 1983), they decide where to live, when to forage and where to forage (Stephens and Krebs, 1986), whether to fight with an enemy or flee from it, and they even make decisions whether to engage in activities that expose them to risk of predation (Lima and Dill, 1990).

Animal decisions can be categorised into preferences and inferences (Stevens, 2008). Preferences rank the desirability of the options while inferences go beyond the information given to make predictions about the state of the world. According to Couzin *et al.* (2006), the decision making and the translation of a decision into an action is not restricted at the individual level. Animal groups like shoals or schools (of fishes), flocks (of birds) and herds (of ungulates) reach group decision and execute it with much accuracy. Animal migration is a spectacular example, where decisions making by animal groups occur in nature (Conradt and Roper, 2005).

Animal decisions have far-reaching consequences in the lives of individuals, population and the community (Lima and Dill, 1990). Making decision, not only affects the quality of life in the next moment but also the cumulative effect of these decisions determine the fate of that animal, species to which it belongs and the structure of the community (Dill, 1987; Lima and Dill, 1990). Thus, the better survivor is the one who is able to reach a beneficial decision by choosing the right and leaving the wrong.

Making a decision

Animal decision making can be explained from several perspectives (Kahneman and Tversky, 2000). From cognitive perspective, the decision making process is regarded as a continuous process integrated in the interaction of animal with its environment. Every decision making process produces a final choice, an action or an opinion. Final decision that is being translated into action is regarded as an outcome of cognitive process leading to the selection of a course of action from among several alternatives (Stevens, 2007; 2008*)*.

From a psychological perspective, it is necessary to examine individual decisions in the context of a set of needs and preferences an individual has and values one seeks. However, behavioural ecologists consider decision making in animals as a process of selecting a course of action from the available alternatives (Dill, 1987). From a normative perspective, the analysis of individual decisions is concerned with the logic of decision making and rationality and the invariant choice it leads to. Yet, at another level, decision making might be regarded as a problem solving activity which is terminated when a satisfactory solution is found, while evolutionary biologists focus primarily on why behavioural decisions exist from a functional perspective (Stevens, 2008). Therefore, Kahneman and Tversky (2000) state that decision making is a reasoning or emotional process which can be rational or irrational, can be based on explicit assumptions or tacit assumptions.

A decision is dissected

Most of the animal decisions are targeted to achieve a goal or a reward (anything that an animal will work to acquire), (Sugrue *et al.* 2005). At any point of time several decision options may be available for an organism for achieving the goal. In such a choice situation an animal has to evaluate different options and select an option that yields the best result. Although, some information may readily be available to make a decision, the decision maker search for more information about possible decision options in order to make its decision most beneficial (Stevens, 2008).

Gathering information

The search for information can occur at internal or external level (Fiedler and Juslin, 2006). Internal level often refers to searching through memories for relevant information about options; where as the external search refers to perceiving information from the physical and social environment. For instance, while foraging from a depleting food patch an animal may retrieve internally from memory of information on the intake rates at other food patches and may track externally the gain and foraging time at the current patch when deciding to leave (Stevens, 2008).

Normally at every moment of life a torrent of stimuli reach various sense organs of the animal. Due to the constraints of the sense organs some of these stimuli are filtered at peripheral level itself. The signals reaching the brain via different sense organs get processed into a single decision. However, in the natural world, usually the information is supplied to the decision maker as a mixture of sensory cues. For example, a male bird presents its courtship displays along with mating calls to attract the female. If the components of a mixed stimulus are separated and presented each cue independently, the resulting behaviour pattern may not have any relation with the original behaviour expected in a parallel context. Similarly, variation in spatial as well as temporal properties of signals can affect the decision making process and its outcome (Hoy, 2005). Hence Hoy (2005) suggests that the major characteristics of a signal considered by the brain, while transforming it into a decision are its spatio-temporal properties.

Decisions are information specific

In a recent study, in Amazon poison dart frog (*Epidobates femoralis*) Narins *et al.* (2005) have demonstrated the influence of cue specificity and how spatio-temporal variation in stimulus modify decision making. In this species, males have enlarged vocal sacs and they make repeated advertisement calls composed of four loud high pitched notes to attract females. During the breeding season male frogs are keen to defend their territory and intruder males will be attacked instantly on entry into the defended territory. When Narins *et al.* (2005) separated auditory cues from the visual cues and presented only the auditory signals (calls) of an intruder male through a loud speaker, the territory holding male was attracted to the source of the auditory signal. On the other hand the sight of a calling silicon model frog (visual cues) in the absence of nuptial call initiated exploration and touching of the model ‘intruder’. However, in both conditions aggressive interactions were not observed. By contrast, when both visual cues and auditory cues are presented simultaneously, the resident male exhibited full-blown aggression and attacked the model.

The influence of spatio-temporal variation in the components of mixed stimuli on the decision making was also demonstrated in another elegant experiment using same model system. Narins *et al.* (2005) desynchronized auditory and visual cues of the intruder male and demonstrated that the resident male is provoked to attack only when the visual stimulus (inflated vocal sacs of silicon model frog) is decoupled from the auditory cue (recorded call) by less than half a second, while longer desynchronization intervals reduced aggressive displays in territory holding frogs.

Influence of spatial relationships of signals on decision making was also analyzed in the same study. Using recorded auditory signals and silicon model-frogs, these authors found that spatial displacement between visual cues and auditory cues interferes with the decision to attack the intruder by the territory holding male. The frog attacked the model only when the distance between the sound (the external speaker) and visual cue (the frog model) were shorter than 12 cm. Hence, Hoy (2005) suggested that similar studies analysing the cue specificity of different decisions in other animal species will be helpful for inferring important perceptual mechanisms like selective attention, sensory binding, sensory dominance and multi modal interactions in processing of a decision.

Processing a decision

Assuming that organisms make optimal decisions, it is pertinent here to ask the question ‘what cognitive process they use in decision making’? It is evident that animals do not calculate a range of expected fitness consequences and apply calculus to find the optimum (Stevens, 2008). Optimal theorists suggest that natural selection acts as optimizing selection process, generating decision processes that result in approximately optimal outcomes (Stephens and Krebs, 1986; Houston and McNamara, 1999; Houston *et al.* 2007)

Tinbergen (1963) suggested that animals handle conflicting situations through hierarchical nervous controls. He assumed that at higher levels, the brain is equipped with mutually exclusive modular processes, so that decision for attacking the prey and fleeing from the predator are taken by two separate modules but the execution of the decision is done through the same set of effecter musculatures. Usually, in binary choice situation, the simplest of conflict situations, the decision is taken in accordance with the anticipated profitability of gain from the choices available. Here, the item or an event furnishing maximum benefit is selected and others are neglected (Matsushima, 2005).

In situations where two options have nearly the same value of profitability the choice will follow the matching law and the animal will shift from one option to the other, as the gain from the selected option recedes (Hernnstein, 1961; 1970). Matching law states that the choices of an animal are distributed according to the rates of reinforcement for matching those choices. The reinforcement is defined as the increase in response probability following a stimulus event. The reinforcement has a greater effect on the motivational status and hence on the decision making ability.

Decision making processes in animals are said to be influenced by another mechanism called satisficing. The word ‘satisfice’ was coined by Simon (1956) as a portmanteau of "satisfy" and "suffice" (be sufficient). In decision making, satisficing explains the tendency to select the first option that meets a given need or select the option that seems to address most needs rather than the “optimal” solution. Recent theoretical studies indicate that satisficing strategies are employed by animals in the context of foraging and mate choice situations (Ward, 1992; Todd and Miller, 1999; Carmel and Ben-Haim, 2005). Additionally satisficing mechanisms yield decisions that are more robust to uncertainty (Todd and Gigerenzer, 2000; Carmel and Ben-Haim, 2005) and can produce nearly optimal outcomes with appropriate thresholds, depending on the costs of information acquisition and level of environmental variation (Todd and Miller, 1999).

Rationality and decision making

Biologists often prefer to explain decision making in animals using heuristic model (Hutchinson and Gigerenzer, 2005). The heuristic approach explains a decision by emphasizing the presence of rules for information search, stopping search, and making decisions (Gigerenzer *et al.* 1999). According to Marsh (2002) animals use the rule of thumb (heuristic) in a number of decision-making contexts, ranging from navigation to nest construction (Hutchinson and Gigerenzer, 2005).

Stevens (2008) suggests two major perspectives on the decision-making process: unbounded rationality and bounded rationality. Unbounded rationality approach considers the decision maker as capable of collecting all information available to reach a decision, producing an optimal result. Here, the decision is attained either by following the rules of logic and statistics or by exhibiting optimal preferences via rules of probability. This model assumes a decision as rational, if it follows the rules of logic and statistics, while a decision taken deviating from the norms of these laws will be considered irrational. Though unbounded rationality approach explains many of the decisions successfully, it presupposes omniscience and unlimited computational power in the decision maker. However, the fact that decision makers are not omniscient and they do not possess or utilize unlimited computational power in day to day decision making, unbounded rationality model is considered as less useful in explaining the process of animal decisions (Stevens, 2008).

Bounded rationality approach did not require any higher level assessment and computation while taking a decision. Instead, it takes into consideration the capacities and constraints, as well as the interaction of the animal and the decision making environment as the basis of each decision (Simon, 1956; Gigerenzer and Selten, 2001). This bounded rationality approach implies a set of computationally simple heuristics that use only partial information to make robust decisions that apply to specific decision making environment (Payne *et al.* 1993; Giegerenzer *et al.*1999). This simple heuristic approach avoids the requirement of extensive information and a higher level statistical device for performing complex computation to make a simple decision.

Brain: the decision processor

Decision making forms the intermediary phase between sensation and action and several investigators legitimately hypothesized that the neural transformations responsible for decision making might exist in brain centres that are linked to sensory-motor systems (Sugrue *et al*. 2005). Sense organs transform sensory stimuli into electric signals and these impulses travel to different centres located in the brain via neural circuitry where it is processed into a decision. It is suggested that inside the brain centers electrical signals undergo three steps of transformation before translated into a decision. First, the sensory transformation mechanism generates a higher order representation from the primary sensory input. Second, a decision transformation system maps these sensory evidences onto probability of one or other operant response. Finally, a process of action is implemented by the motor centers through the motor neurons, which are expressed in the form of behaviour (Graham, 1989). Hence, most of the studies that analyzed the neurobiology of decision making tried to trace out this key link between sensory and motor areas of cerebral cortex, with a hope of finding the centers involved in the neural processing of the decision (Rizzolatti and Luppino, 2001; Leon and Shadlen, 1998; Schall, 2001; Glimcher, 2001). Recently, the role of different areas of cerebral cortex in the processing of decision is elucidated with remarkable accuracy (Sugrue *et al*. 2005).

It has been demonstrated that many neurons of prefrontal and parietal regions of cortex receiving sensory inputs, projects to motor planning centres and are reciprocally connected to the dopamine system directly or through the striatum. This connection with the major motor centres within the brain makes the cortical area a central processing unit of decisions. In this area, sensory signal is value transformed (a process by which stimuli or actions are scaled for their value of utility to the animal in an internal model of the world) to compare with the internal scale, to reach a beneficial decision. This value transformed sensory signal is called a neural currency and brain reaches a decision by comparing the value of neural currency generated from the signals perceived with the already existing value chart self-organized from the experience and expectation (Sugrue *et al*. 2005). These transformations were studied in monkeys that have been trained to discriminate noisy visual stimuli and report their perceptual judgments using eye movements. By recording neural activity in visual and oculomotor pathways during such tasks, investigators have identified sensory representations, as well as decision related signals in areas of the parietal and frontal cortices (Sugrue *et al*. 2005).

Dopamine neurons in decision making

According to Powell (2003), variation in the activity and functional properties of neurons can impart concomitant variation in the assessment of a situation and decision making. This is because, certain neurons can indeed code for some of the variable weighed during simple decision or choice. Though many types of neurons in the brain could be attributed with the power to influence decision making, the dopamine neurons are the most studied cells in connection with neural processing of decision. The process of conversion of a sensory signal in to a value based neural currency and its translation into a decision is taking place under the strict critics of dopamine neurons located in mid brain region (Dayan and Abbot, 2001).These neurons are shown to have a reinforcing effect, so that the animal will seek out stimuli that are followed by the release of dopamine (Fiorillo *et al*. 2003). Moreover, the continuous excitation of these neurons could alter the normal decision making ability of an animal by affecting reward seeking behaviour. The increased activity of dopamine neurons during the uncertainty about a reward shows that an uncertain situation presents a learning opportunity that may help the decision makers to "beat the odds" the next time they face it (Powell, 2003).

Lateralisation of brain makes decision making easy

Recent evidences suggest that the right and left hemispheres of the brain are specialized for handling antagonistic behavioural responses in a good number of animal species (Vallortigara and Rogers, 2005). This asymmetry in the brain is also reflected in a variety of left-right perceptual asymmetries among vertebrates. Animals as different as fish, amphibians, reptiles, birds and mammals appear to be more responsive to predators seen in their left visual field rather than their right hemi-field (Vallortrigara *et al*. 1999; Rogers, 2002). In contrast to their leftward responses to predators, animals preferentially use right visual field and right hemisphere for feeding responses (Vallortrigara and Rogers, 2005). According to Vallortrigara and Rogers (2005), animals with lateralised brain are more efficient and hence reach quick decision compared to their conspecifics with a non-lateralised brain. Hence, Matsushima (2005) postulates that the advantage of brain lateralization could have been helpful in quick processing of incompatible functions by reducing the probability of delay in response due to conflict.

Decision, action and outcome

The decision processed by the brain is decoded into an action by motor nervous system. The expression of a decision initiates behaviour, either an inference or a choice. The moment at which a decision is converted to an action, it comes under the strong selective force of the evolutionary pressure. The experience gained by the animal is stored in the memory to be utilised later, while making decisions later. According Stevens (2008), selection forces of nature will try to optimize under constraints and hence he predicts that an optimal decision will go hand in hand with optimal selection. Therefore animal that use decision processes approaching the optimal outcome transfer more genes to future generations.

How an evolutionarily suitable decision is made

A decision is not inheritable, how much beneficial it may be. Moreover, there is no decision termed optimal decision, as the fitness value of the same decision may vary from context to context. Hence, the only inheritable part of the decision, the mechanism involved in the processing of a decision, experience intense intervention by the evolutionary forces. The three feedback mechanisms that shape evolutionary suitability of decisions made by an animal are natural, selection, reinforcement learning and the functional evaluation (Stevens, 2008).

Natural selection

Natural selection determines the evolutionary fitness of a decision by evaluating its outcome or consequence (Stevens, 2008). Here, organisms bearing genes coded for the ability to make better decision are selected and promoted by the nature. Specifically, natural selection favours genes for decision processes that result in good decisions, actions and outcomes from a fitness point of view. To determine whether a decision is good or bad, a selection process must evaluate the outcome relative to some criteria. Hammond (2000; 2007) described two types of selection criteria: correspondence and coherence. Correspondence refers to the degree to which decisions achieve empirical accuracy; that is, whether they reflect the true state of the world. For instance, we can evaluate an inference about how fruit color relates to sugar content, based on how well this inference corresponds with the true relationship between color and sugar content. Alternatively, coherence refers to following some norms, usually rational norms such as Bayesian reasoning and expected utility theory. An inference about fruit color and sugar content can not only correspond to the state of the world; it can also cohere to a Bayesian analysis of an individual's prior experience with color and sugar content.

The drawback of natural selection in shaping a perfect decision making mechanism is the slow pace with which it tracks the changing environment. Moreover, genetically coding of all decisions mechanisms would leave organisms poorly adapted to their environment. In this context brain mechanisms like reinforcement learning and functional evaluation help animals to quickly adapt with the current situation, without waiting for commands from genes. Dawkins (1976) points out that brains are not slaves of the genes but neural mechanisms allow animals to process information and execute actions flexibly. Stanovich (2004) considers those decisions that come under direct influence of genes as highly restrained whereas, decision process involving brain mechanisms are more flexible in executing the decisions.

Reinforcement learning

Learning is a process that allows considerable flexibility in decision making of an individual. Skinner (1938) had demonstrated that a positive reinforcement increases the frequency of behaviour, while a negative reinforcement decreases it. In evolutionary terms, reinforcement learning is often linked to evolutionarily significant objects or events. For instance, any behaviour that yields more food, water or mate will definitely increase the fitness of the animal.

A brain mechanism that functions based on this correlation is advantageous to the animal and allows fitness maximization to achieve a good evolutionary result (Stevens, 2008). However, operant conditioning, often mistaken with reinforcement learning does not influence the decision process itself, but simply the frequency of an action (Williams, 1994). In contrast, reinforcement learning operates at the level of the decision processing (Rieskamp and Otto, 2006). Thus decision makers can learn to implement different decision processes based on feedback from the outcomes received. Reinforcement learning can then adapt either actions or the decision process itself to the reinforcement contingencies in the environment. (Stevens, 2008).

The reinforcement learning helps animals to adapt to a situation with in a short duration of time. This lag could be considered negligible in comparison to the time required for the action of natural selection. The reinforcement learning enhances the fitness of an animal by reducing the time required for taking a decision in a situation already experienced earlier. Though, learned facts are not inherited, the social transmission of it by way of social learning could be beneficial for the whole community.

Functional evaluation

Functional evaluation is a process which adds more flexibility for decision making in comparison to natural selection and reinforcement learning. Natural selection and reinforcement learning are two mechanisms that operate on the outcome or consequence of a decision. On the other hand, functional evaluation is a mechanism that selects, not based on previous outcomes, but on the behaviour to achieve a reward or goal. Using functional evaluation, a decision maker mentally evaluates the decision options available and chooses the one with the potential to maximize the relevant selection criterion. Instead of maximizing the fitness or reinforcement value, functional evaluation assesses potential actions and outcomes relative to the decision goal. Functional evaluation can occur at either conscious or subconscious levels. Precisely it refers to the selection process in which outcomes are evaluated before they are experienced (Stevens, 2008).

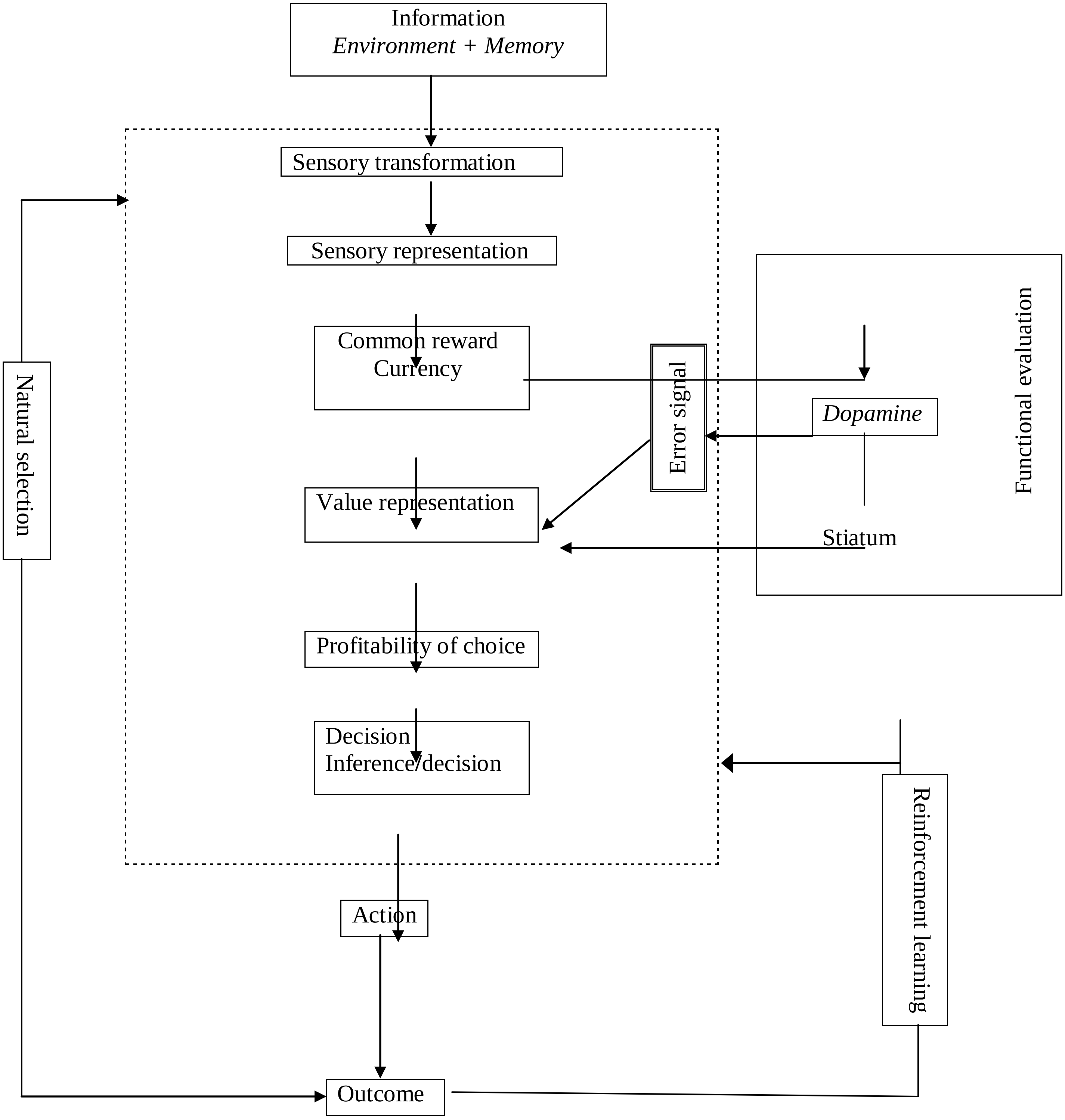

Figure 1. Decision mechanism and selection processes

Group decisions

In social species, individual members of a group will have to reach a unified decision and to work for a single goal by avoiding conflict between the members. For example, a shoal of migratory species will have to reach a unanimous decision about a target location and route (Krause *et al.* 2000). In animal societies, group decisions can result from combined decision making or from consensus decision making (Conradt and Roper, 2005). In combined decision making, members of group choose individually between two or more actions. Even though, combined decision making does not aim for a consensus, the consequence of the decision usually affect the group as a whole. This decision making system is not free from conflict among the members and the members will decide freely in no conflict situations whereas, the members will fight for the control in conflicting situations. This conflict for the control is the major cost paid by the societies that follow the combined decision strategy for a group decision. Task allocation in eusocial insects, where individuals take up tasks such as foraging or nest cleaning according to local necessity (Beshers and Fewell, 2001) and group joining and leaving in fission-fusion societies of birds (Clutton-Brock, 1998) and fish shoals (Krause *et al.* 2000) are excellent examples for combined decision making.

Consensus decision making occurs, when members of a group choose between two or more mutually exclusive actions with the aim of reaching a consensus. The best example for consensus is seen when a flock of birds decide to leave a foraging patch (Black, 1988) or a group of primates deciding destination and route of journey after a period of rest (Stewart and Harcourt, 1994). While practicing consensus decision making, though all members will follow the decision, it is not necessary that all members should equally contribute to the decision making. In the selection of a nest site by eusocial insects (Seeley and Visscher, 2003; Conradt and Roper, 2000) or in the decision to leave a depleting patch, the element of conflict is negligible as all members possess similar goal (e. g. best nest site, best route etc.).

In many animal societies a consensus is reached not peacefully as in a bee hive bird flock. The major reason of conflict among individuals (the consensus cost) is the difference in the optimal timing of activities and the variation in the preferences of individual group member (Krause and Ruxton, 2002; Prins, 1996; Rucksthl, 1998; Gompper, 1996). Hence, when a group takes a decision between mutually exclusive activity like resting or moving (Conradt, 1998; Rucksthl, 1998; Gompper, 1996) or between moving to different sites offering food or water (Stewart and Harcourt, 1994; Black, 1988; Milton, 2000; Byrne, 2000), the individual preferences can ignite conflict incurring a consensus cost.

The consensus decisions are classified into two types:

(a) The decisions involving conflict of interest between group members

(b) The decisions involving either local or global communication between group members.

a) *Decision involving conflict*

The compulsion to deviate from optimal timing of activities to sub optimal level can lead to consensus cost to a group member, which could initiate conflict before reaching to a consensus (Conradt, 1998). If this consensus cost rises above a certain level, the conflict may escalate leading to the splitting of the society. Hence, Conradt and Roper (2003) postulates that, in sexually dimorphic animals like African ungulate species usually exhibit inter-sexual social aggregations due to the inability of the sexes to cope with consensus cost (Ruckstuhl and Neuhause, 2002).

Additionally, the factor, 'who makes the decision in a group' can also influence conflict and co-operation during process of consensus decision making. This is because if the decision maker is dishonest or selfish, the outcome of such a decision can affect the fitness consequence of the whole group. According to Conradt and Roper (2003), there are three possibilities concerned about the identity of the decision maker in a consensus decision. First, a decision could be made in an equally shared manner, whereby, all group members contribute equally to the decision, independent of their individual identities or social status. In this type of decision making, consensus is usually reached via a quorum (majority, sub-majority or super majority of members, Franks *et al*. 2003) or by averaging over all votes (Seeley and Visscher, 2004; Prins, 1996). Second, the decision could be made in an intermediate manner (partially shared, ranging from little to widely shared), where a demographic subset of members contribute more to the decision than do others. Third, the decision could be unshared, that is taken by a single dominant animal, with all other members abiding by its decision. In such situations, coercion by the dominant animal is the suspected mechanism for resolving conflict. However, coercion is unlikely to work, as the gain from coercion usually will not out weigh the cost of coercion. Thus, it could be concluded that the animals reach a consensus decision through voluntary compliance to either unshared, partially shared and equally shared decision making rules (Conradt and Roper, 2005; Simons, 2004; Kummer, 1968).

b) Decision involving communication

Even though, there may exist conflicts about the decision among the members of a group during the decision making, the decision is to be communicated among the group members so as to convert it into a fruitful action. Reaching consensus decision by a group is highly dependent on the effectiveness of the communication. According Conradt and Roper (2005) the communication system found in animal groups can either be global communication or local communication.

In global communication each group member can communicate with all other members. The global communication is usually observed in social primates (Ruckstuhl and Neuhans, 2002), carnivores (Clutton-Brock *et al.* 2001) or ungulates (Ruckstuhl, 1998, 2000), where the society is comprised only of a small number of individuals. However, this type of global communication is not possible in societies with large number of individuals (e.g. honeybee colonies, shoals of fishes etc.). In such societies information transfer is taking place via the communication with spatial neighbors (List, 2004; Huse *et al.* 2002). In such groups, the consensus decision is a product of self organizing rules. Self organizing rules are the behavioural rules that individuals can follow using only local information and which result in an organized group behaviour without the need for global control (List, 2004; Seely and Visscher, 2003). Thus, whatever the mode of communication seen in the animal community (global or local communication) be, the unshared or badly informed decision can be disadvantageous to the decision maker as well as to the society (Franks *et al.* 2003) whereas, equally shared decisions rarely profit all members to the same extent (Conradt and Roper, 2003).

According to Surowiecki (2000), the decisions taken by considering the information provided by the individual members of a group are more accurate than the decisions made by a single decision maker. The reason behind this ‘wisdom of crowd’ is that, every group member has some information relevant to the decision. Though, there may be error in the information provided by the individuals, the pooling of information may produce a more accurate decision outcome, which results in fitness advantage to consensus decision makers (Seeley and Visscher, 2004; Franks *et al*. 2003).

DECISION MAKING IN FISH: A HISTORICAL PERSPECTIVE

Like other animals living in the wild, fishes are also put constantly in conflicting situations which they resolve by taking appropriate decisions. Some of the well studied circumstances where decision making and choice occurs in fish are what to eat and what to avoid, which route to take for a profitable foraging trip, whom to approach and from whom to keep away, whom to mate with and whom to fight with (Laland, *et al.* 2003). Genetically determined predispositions and instinctive responses often allow the fish to take appropriate decisions in several occasions. Many species of fish do not require any experience in order to recognize and respond to visual cues from their natural predators. For example, predator-naïve paradise fish (*Macropodus opercularis*, Belontiidae) show a stronger reaction to sympatric predators than to allopatric predators (Gerlai, 1993). Moreover, Humbug damselfish (*Dascyllus aruanus*, Pomacentridae) can discriminate piscivorous and non-piscivorous heterospecifics (Coates, 1980). However, many of the decisions are the product of learning and the experience acquired by the fish during its

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Lateralized processing of information in fish brain

Similar to other advanced vertebrates, fishes also use different brain hemispheres for processing biologically significant information about mate, conspecifics, rivals and novel objects in their habitat (Vallortigara and Rogers, 2005; Bisazza *et al.* 2000). According to Brown *et al.* (2004; 2007), the poeciliid fish *Brachyraphis episcopi*, utilise their right eye (left hemisphere) for the assessment of conspecifics while the left eye (right hemisphere) for evaluation of a novel object in its habitat.

The utilization of right eye connected to and communicating with the left hemisphere of the brain through the optic chiasma for the assessment of the shoal of opposite sex or a predator (Bisazza *et al.* 1998) has been reported in different fish species. Bisazza and de Santi (2003) have demonstrated that all the three species of fishes they tested (*Gambusia holbrooki*, *Xenoteca eiseni* and *Betta splendens*), utilize their right eye to assess the rival before reaching a decision to attack. This study revealed that the direction of asymmetry in the brain utilization during the assessment of rival by fish is opposite to that shown by all other vertebrates

According to Bisazza *et al.* (1998), the degree of lateralization exhibited by a species varies with gender and can fluctuate depending on the experience acquired in a habitat (Sovrano *et al.*, 1999). Difference in lateralized brain use in decision making is obvious both in solitary and social species. Moreover, the motivational status of the decision maker can also affect lateralized use of brain during decision making. For example, lateralization was found to be enhanced in females of poecilid fish viewing a shoal of males, if they were deprived of male contact for two months (Bisazza *et al.* 1998). Brown *et al.* (2007) hypothesized that the difference in the pattern of brain lateralization observed between fish species and population within a species are due to the manner in which they perceive and classify stimuli in the world around them and in particular, the perceived emotive content or context of a scene is likely to vary between individuals that have had different life experiences.

Neurobiology of decision making in fish: The role of Mauthner cell (M cell)

Hypocampal pallium or and amygdalarpallium are shown to be the brain centres that control various aspects of learning in fishes (Rodriguez *et al.* 2006, 2005; 2002; 1994; Lopez *et al.* 2000). Majority of the studies dealing with the neuroboiology of decision making in fish are centred on the function of Mauthner cells or M cells (Korn and Faber, 2005). M cell is considered to be a miniature brain (Stevekuller quoted in Korn and Faber, 2005) or a command neuron, because the firing of this cell is necessary and sufficient to trigger a complete behavioural act like the escape response.

M cells receive information about the danger via auditory input, visual input and octavolateralis system (lateral line, vestibule etc. (Faber and Korn, 1978). After receiving such a signal carrying the information about the emergency, decision by the M cell to fire and trigger a specific motor reaction leads to the performance of the escape behaviour. When one of the M cell fires, the fish will exhibit the fast-start escape behaviour, ‘C start’ ; so named on the basis of the shape of fish at the first stage (stage 1) of this reflex, before forward propulsion (stage 2) (Eaton *et al.* 1988; Zottoli, 1997). In this perspective, the decision level for the escape could be considered equivalent to the firing threshold of one M neuron and the likelihood of reaching the threshold depends upon external conditions (Schall and Thompson, 1999).

During a C start escape behaviour, the animal changes its orientation away from the startling stimulus (Korn and Faber, 2005). The extend of this response, as well as its variation, are controlled by the interaction between the components of neural network, comprising the activated M cells and its homologues MiD2 cm, MiD3 cm and other descending reticulo- spinal neurons (Eaton *et al.* 1984; Di Dominico *et al.* 1998; Casagrand *et al.* 1999). Moreover, the stage one (C start) of the escape response is with high variability in duration, angular displacement and distance moved. The variability of these phases is the consequent difference between size of the initial agonist muscle contraction and that of later antagonistic muscle contraction, as well as the timing between the two contractions (Eaton *et al.* 2001). The resulting unpredictability about the escape path is in marked contrast to the direction taken by a predator aiming at its prey and this important feature of the M cell triggered escape decision make it difficult for a predator to adapt or to learn a successful strategy for prey capture.

The independent selection of trajectory during the ‘C start’ response by a solitary fish changes dramatically when it joins a shoal. In a shoal, the variability in the trajectory of C start response disappears and all members will choose a single trajectory during predator attack. This behaviour modification enhances the synchronization of group manoeuvres and avoids the collision between the members during the performance of antipredator strategies (Domenici and Batty, 1997). Additionally, Korn and Faber (2005) suggest that the presence of certain visual stimuli like physical barrier or obstacles also can modify the escape direction during a predator attack. Hence, Glimcher (2002) suggest that the environmental problems animals experience shape not only their decision making ability and behaviour, but also the neural hardware that generate the behaviour.

Eating decision

Most of the literature dealing with behavioural ecology of animals, including fish reveals that foraging is the most vital behaviour determining the fitness of a species. The foraging decisions of a fish could be considered as the most essential one, but these decisions exhibit marked variability in accordance with the spatio-temporal quality of the habitat, as well as with the social status of the decision maker. The foraging decisions can vary from a simple biting response to complex processes like taking a decision in a binary choice condition or feeding under the threat of a predator. The major factors determining the foraging decision of a fish are:

a) *Motivation*

The motivational status can affect the foraging decision and its translation into an action. The major components comprising the motivation of a fish to feed are drive (deprivation level) and stimulus attractiveness (incentive value; Lieberman, 1990). The hungry fish is more prone to take risky decision to get a food item and the hunger reduces the distraction and influences of the external and internal factors on the foraging decision of a fish (Milinski, 1993; Reader and Laland, 2000). In addition to the physiological factors like hunger the socio-biological factors like isolation, presence of conspecifics and the ecological parameters like water quality, presence of fear evoking stimuli like predator can affect the motivational level and thus the foraging decision in fish (Jain and Sahai, 1989; Griffiths, 2003; Kelly and Magurran, 2003).

b) Cognition

Being an organism with high level of cognitive ability, fishes exhibit flexibility of response and goal directed actions while taking an active decision during a foraging session (Dickinson, 1994; Chase, 2001). They can actively anticipate and expect a food item and can remember and come to feed at a particular location at a particular time of a day. Reebs (2000) demonstrated that the golden shiners display daily food anticipation activity and learned to expect food at midday in one of the brightly lit corners of their tank. Fishes can actively remember the conspecifics with which they achieved the feeding success and consider the presence of such conspecifics, while taking a foraging decision (e.g. Bluegill sunfish, *Lepomis macrochirus;* Dugatkin and Wilson, 1992). However, Persson, (1985) points out that fishes have difficulties while taking a decision to achieve simultaneous exploitation of food sources demanding different feeding strategies (such as those required for different types of prey).

c) Competition

The pace and performance of the decision making may influecne the ability of fish to compete with conspecifics and heterospecifics. The relative pay-off of some learning rule predicts that good competitors will decide where to feed earlier and switch less between patches than poor competitors (Regelmann, 1984). Johnsson (1997) demonstrated that in rainbow trout the aggression, food intake and growth rate are positively correlated with dominance and the ability to compete. Additionally, this species can recognize and remember its potential competitors and will always avoid escalation of fight with dominant fish for the control of feeding territories (Switzer *et al.* 2001; Johnsson, 1997).

d) Risk

Presence of a predator or any stimuli indicating risk affects or abolishs the foraging motivation of a fish. There is evidence that fish continually adjust their behaviour in accordance with a risk–balance, forage–refuge trade off, to avoid being prayed upon when they are feeding (Mittelbach, 1981; Pitcher *et al.*1988; Milinski, 1993). When both demands are conflicting (i.e. maximizing food intake is achieved only at the expense of efficient avoidance of predation and vice versa), it has been shown experimentally that fish make a compromise by fulfilling either or both needs less efficiently. They take a greater risk in order to feed more efficiently when the need for food is increased by starvation or by parasites, or when feeding is much more rewarding in places with predators (Mlinski, 1993). Diet selection within a patch can be altered, if one type of food is riskier to feed upon than others. Smaller fish experiencing increased risk of predation accept less rewarding food in order to avoid the predator, than do bigger fish.

By foraging in large shoals, fish can detect and monitor an approaching predator more easily and efficiently and continue feeding for longer in presence of a predator than fish in smaller shoals (Pitcher and Parrish, 1993). Milinski (1993) points out many studies demonstrating the qualitative and quantitative evidences for teleosts changing their behaviour adaptively when costs and benefits of feeding and predator avoidance vary. Because of the difficulty in measuring all costs and benefits and knowing how accurately the fish may do this, it is difficult to predict the compromise-behaviour quantitatively.

Mate choice decisions

As the quality of mate can affect the quality of progeny and thus the fitness, choosing the mate is one of the crucial occasions of decision making in the whole life history of a fish. Turner (1993) classified mate choice decisions of fishes into two categories:

a) Choice for immediate benefit

b) Choice for good genes

a) Choice for immediate benefit

No matter which sex they belongs to, individuals investing more energy and resource in reproduction are choosier about their mate and take a decision after assessing the qualities of the available opposite sex. Normally the investment of male in reproduction is less, as compared to that of the female. As the males produce large quantity of gametes, most of the fishes exhibit polygynous mating system. An exception to this rule is the males of species exhibiting complete or partial parental care. In the majority of fishes, males and females select their mate using body size as a criterion. For instance, males of three spined sticklebacks (Sargent *et al.* 1986), Gobi (*Chaenogobius issaza;* Hidaka and Takahashi, 1987) etc., prefer large, fecund females. The females of

Cichlasoma citrinellum always mate with larger mates. The only exception for the selection of largest among the mates available is reported in mosquito fish, where males devoting more efforts to smaller females (Bisazza *et al.* 1989).

Male fishes consider sperm competition, while taking decision to mate with a female. Usually, males of livebearing fishes choose virgin female or those that have recently given birth (Bisazza *et al.* 1989; Farr and Travis, 1986). According to Turner (1993), selection of such recently given birth females are done with the help of male stimulating pheromones produced by the female, another factor affecting the mate choice decision of male fish.

In those species, where males exhibit nest building and parental care, the female assesses the quality of the nest constructed by the male before reaching a decision to share her genes with displaying male (Downhower *et al.* 1983; Bisazza and Marconato, 1988a and b). Here, the nest building capacity acts as an ornament and males constructing better nests are always selected by the fecund females. In damsel fishes (*Stegastes dorsopunicans* and *Microspathodon chrysurus,* Peterson 1990) and wrasse (*Symphodus ocellus*, Wernerus *et al.* 1999), female mating decision is influenced by the experience of the male, and females always choose the experienced males. The reason behind such a decision is that the experienced male performs reduced level of egg cannibalism and produces more offspring due to their past experiences. Hence, females of bulhead gobby, *Cottus gobio* (Marconato and Bissazza, 1988a;b), fathead minnow, *Pimephales promelas* (Unger and Sargent, 1988) always take a decision to lay their eggs in nests already having eggs.

b). Decisions favouring better genes

Many species of fishes take mate choice decision with long term benefits, they choose partners possessing best genes (Turner, 1993). For example, females of guppies (Houde, 1999; Breden and Stoner, 1987), sticklebacks (Mc Lennan and Mc Phail, 1990) and cichlids (Hert, 1989) prefer highly ornamented males. According to Zahavi (1975) the ornaments are the honest displays of male qualities like vigour and good genes. Furthermore, Hamilton and Zuk (1982) and Milinski and Bakker (1990) have demonstrated that the ornamentation of male is correlated with the parasite status, and only the less infected males possess colourful ornaments.

Another quality affecting the mate choice decision by the female fish is the aggression and boldness of the male. Usually, the bold male defend territory with better quality and choosing such a partner with good genes can help the female to enhance the quality of her lineage (Godin and Dugatkin, 1996). Such a preference for males holding areas with higher safety as their territory is exhibited by wrasse (*Halichoerus melanochir;* Moyer and Yogo, 1982), where females compete to mate with males holding a central territory.

c) Other factors correlated with mate choice decision

As in the case of advanced vertebrates like birds and mammals, sexual imprinting can influence the mate choice decision of a fish (Witte, 2006). The sexual imprinting is defined as the learning process restricted to a short and specific period during the development (Immelmann, 1972). Sexual imprinting hypothesis is supported by the results from cichlids, were parental colour morphs influences the mate choice decision.

In Malawi cichlid (*Pseudotropheus sp.*), the males always preferred to mate with females possessing coloration similar to that of their mother (Pierrotti, 2008). Hence, Witte (2006) states that the sexual imprinting can influence the mate choice and the copying of such decision by other individuals of a population may end up in sympatric speciation. However, in some other fishes the sexual imprinting has no influence on the mate choice decision. They learn the quality of mates through experience (e.g. guppy, Haskins and Haskins, 1950).

In Siamese fighting fish, the female's decision about a mate is guided by the information gained by eavesdropping (Doutreland and McGregor, 2000). Evesdropping occurs when information from animal transmitting signals to another animal is overheard and utilized by one or more bystanders, towards whom the signal was not directed (McGregor, 2005). The females that observed an inter-male conflict will always choose the winner male to mate with (Doutreland *et al.* 2001). The dependence on eavesdropped information is beneficial to the decision maker, as the information is offered for no cost (McGregor and Peake, 2000).

There are contexts in which the mating decision taken by one fish not only influences the decision of another fish, but the latter just copies the decision of the former (Witte, 2006). This phenomenon commonly known as mate choice copying is practiced by species like guppy (Godin *et al*. 2005), the humpback limia (*Limia nigrofasciata,* Munger *et al.* 2004), sailfin molly (*Poecilia latipina,* Witte and Ueding, 2003) etc. In these species the interactions between a male and female influence the subsequent mate choice decision of another individual observing them. Here, the observer just copies decision of observed mating individual (Witte, 2006). As in the case of eavesdropping, in mate choice copying also the imitator gets the information without any risk and in the absence of investing even a single calorie of energy. The major risk with copying the decision of another female is the reduced fertility resulting from sperm depletion in male when the copying female mates with a male that has already courted with several other females (Witte, 2006).

According to Pruette–Johnes (1992) copying mate rejection is also found in fishes. Witte and Ueding (2003), have demonstrated that sailfin mollies always avoided the males which have been rejected by any other females earlier. It has been demonstrated that the social decisions can influence the genetically encoded mate choice criteria (Dugatkin, 1998). Using female guppy model system, this author has demonstrated that the inherited preference for brighter males could be changed, if the female observes a drabber male surrounded by two females. Observing such a drabber male (usually avoided by the female), the females will move around that male for mating. Hence it could be concluded the mate choice decision making is a complex process involving not only the genetic factors (Bakker, 1999), but also non genetic factors like social environment (Dugatkin, 1996; Westneat *et al.* 2000) and learning (Danchin *et al.* 2004).

Individual variation in decision making

According to Magurran (1993), there can be considerable variation between (and even within) individuals in a whole host of behaviours, including decisions they take during foraging, predator avoidance, and selecting a mate. This variation can be seen even among the members of a school, the most egalitarian and uniform piscine societies (Shaw, 1978), as well as in the performance of instinctive behaviours like attacking a red dummy by the male stickleback (Rowland, 1995). Individual variation in decision making and handling of conflicting situations via trade-off is highly significant from the evolutionary point of view, as this may function as a starting point for the evolution of sympatric species (Darwin, 1859; Parker, 1984; 1985).

Differences with in an individual

The flexibility in the decision making ability of a fish is often linked with the morphology, predator regime, and social dominance (Magurran, 1993). This individual variation in the morphology and associated variation in the propensity to take a (risky) decision is evident in the study of Reist (1983) using brook stickleback (*Culaea inconstans*). In Canada this species can be seen with variation in their pelvic skeleton and associated spines (varying from morphs where it is complete through a range of intermediate forms to morphs where it is totally absent). Reist (1983) found that sticklebacks without spines were more vulnerable to predation and were less interested for decision flexibility.

The factors like age, longevity and life expectancy can influence the decisions made by a fish (Magnhagen, 1990) since, the increase in age is correlated with the increase in size, variation in physiological state, hormone profile etc. The effect of variation in decision making ability with increase in age is evident in the reproductive decisions of black goby (*Gobius niger*), in presence and absence of a cod predator.

Young male gobies (2-3 three year old) significantly reduced their nest building activity when exposed to the cod predator. By contrast, old males (4-5 years old) always ignored the predator and continued to build nest in presence of the predator.

Individual experience is another factor that influences the decision making ability of a fish. The experienced fishes will take a decision by considering the reward or punishment obtained from a similar situation. Such decision modifications resulting from experience are evident in the operant conditioning experiments (Rodríguez *et al.* 2006) and social training of fishes using demonstrators (Brown and Laland, 2001). Here, the experience of demonstrators can affect the decision of observer and in many contexts and the observer may blindly follow the decision of demonstrator (Reader and Laland, 2000).

One of the most dramatic shifts in behaviour and decision making ability of an individual arises when the fish changes its sex (Shapiro, 1979). Sequential hermaphroditism is reported in 13 families of fishes and provides a mechanism for individuals to adjust their reproductive output to the social structure of the group that they belong to (Turner, 1993). In blue headed wrasse (*Thalassoma bifasciatum*), the mating territories are defended by large males. Hence, due to the inability to compete with dominant male, an individual starts its life as a female and change its sex when it grows beyond the size of the dominant male. In anemone fish (*Amphiprion akallopsis*), an exact reversal is taking place. Here, the small fishes are males and they will change to females when they grow, because only large females can harbour more eggs (Fricke, 1979). Hence, the sex change and its consequent variation in the physiological states and decision making abilities provide an excellent area for the future research on decision making (Magurran, 1993).

Presence of a fish near by, no matter whether it is a conspecific or heterospecific, can influence the decision of a fish (Jain and Sahai, 1997). The individual variation in decision making is very low in members of shoals or schools compared to a solitary species. However, Magurran and Pitcher (1987), point out that the behaviour of a shoal member is contingent on the group size (defined as number of individuals present in the group). For instance, the minnows in groups of ten are more likely to abandon and decide to seek cover, if attacked, than a school of minnows with 50 or even 20 colleagues in the vicinity (Magurran, 1993).

Variation between the individuals

Behavioural flexibility of an individual fish is clearly appropriate in an environment with inconsistent properties. Similarly, when populations are isolated, either geographically or reproductively and subjected to selection pressures with variation, individuals with a mosaic of behavioural variation will emerge. A well explored case of population variation in decision making is provided by a study based on guppies inhabiting different aquatic ecosystems with variation in the degree of predation pressure (Magurran and Seghers, 1990). The guppies which usually live in shoals avoid grouping strategy and always found solitary, when the pressure of predation increased. These results show that in a dangerous habitat guppies switched their inherited decision of joining a group towards living in solitude, since the predators are attracted to a fish group easily rather than towards a solitary fish.

According to Magurran (1993), dominance status and health condition of individuals can also influence their ability to take decisions. For instance, in sticklebacks infected with microsporidian sporozoa, *Glugea anomala* or a cestod, S*chistocephalus solidus*, the percentage of foraging decision was always biased towards smaller preys (Giles, 1983), a condition rarely seen in normal fishes. Milinski (1993) have shown that the parasitized sticklebacks always exhibited enhanced propensity to take risky decision like feeding in presence of a predator.

Sex and decision making

Gender difference can influence behaviour patterns not immediately associated with reproduction. Abrahams and Dill (1989) examined the foraging decisions of male and female guppies in presence of a predator. The results revealed that only females were willing to accept greater danger in exchange for higher energetic cost. Additionally, female guppies were more innovative in foraging tasks (Reader and Laland, 2000) and learned different tasks rapidly than the males (Reader and Laland, 2000) and novel foraging information spreads more rapidly through female than male sub groups (Reader and Laland, 2000). By contrast, the tendency to take a risky decision of exploring a novel area was very little in females of poeciliid *Brachyraphis episcope,* compared to males (Brown *et al.* 2005). In this species, the males took quick decision to emerge out of the shelter provided while, females exhibited a significantly higher level of latency to reach and execute the same decision. Brown *et al.* (2005) put forward the following hypothesis to explain this gender variation in the decision making ability. ‘The males always tried to increase their fitness by inseminating maximum number of females, while females protect themselves from predation and other risks to increase fitness by living for a longer period.

Decision to fight

Aggressive interactions are a common means of contesting for resources in most animals (Hsu *et al.* 2006). A fish is compelled to fight in many contexts during its whole course of life. The decision to fight by a fish is influenced by a number of factors like hunger, size, residency and age (Beaugrand *et al.* 1996; Hsu *et al.* 2006). Among these factors, prior contest experiences influence the individual perception of its own fighting ability and hence the decision to fight (Hsu *et al.* 2006). Victorious individual fish is more likely to take quick decision to attack or retaliate and escalate contest when attacked. By contrast, the looser is less likely to initiate the fight and are more likely to retreat even when attacked. However, the effect of experience on reaching a fighting decision is negatively influenced by the body size asymmetry of contestents (Beaugrand *et al.* 1991), prior residency (Beaugrand *et al.* 1996), and energy reserve (Marden and Waage, 1990).

Eavesdropping, the act of extracting information from contest interactions between others (Peake and McGregor, 2004; Peake, 2005), can also determine the fighting decision of a fish. In Siamese fighting fish (*Betta splendens*) and green swordtail (*Xiphophorus helleri*), observers appear to update their perception of the fighting abilities of the watched individuals based on the dynamics and/or outcome of the witnessed contest (Brown and Laland, 2003; McGregor *et al.* 2001). Hence, Dugatkin (2001) states that there is some indications that indirect experience and subsequent adjustments of perceived relative fighting ability by an eavesdropper, reinforces linear hierarchy and thus reaching a quick fighting decision and its instant execution.

The transitive inference in the fighting context refers to the ability of an individual to combine individual experience with a particular opponent and information obtained through eavesdropping. Recently Grocenick *et al.* (2007) have demonstrated that the males of cichlid *Astatotilapia burtoni* possess the ability for transitive inference and can successfully make inference on a hierarchy implied, by observing pair-wise fight between rival males. These fish learned the implied hierarchy vicariously (as bystanders) by watching dyadic contests. Grosenick *et al*. (2007) suggest that fish can make inference using indirect information alone and have both spatial and featural representation of rival's abilities, which they can use to make correct inferences depending upon what information is available to them.

Decision to cooperate

Though, once considered as organisms with lesser levels of cognitive ability and having no ability to cooperate (Wilson, 1975), recent results obtained from different species have shown that fishes also cooperate to achieve goals (Alfieri and Dugatkin, 2006). Social co-operation results when two or more individuals decide and behave in a coordinated manner and as an outcome, participants gain some type of benefit (positive contribution towards one's fitness). The benefit may be direct (gaining a meal, a valuable piece of information or protection from predator) or indirect (improving the survival of kin or increasing the possibility of future benefit, Alfirei and Dugatkin, 2006; Sachs *et al.*2004; Stevens and Hauser, 2004). Dugatkin (2001) considers the ability to take a decision to cooperate as a complex cognitive trait requiring many types of cognitive abilities. Based on the origin and maintenance, the co-operation systems in fish are divided into four categories, kin selection (Hamilton, 1964 a; b), reciprocity (Trivers, 1971; 2004), byproduct mutualism (WestEberhard, 1975; Brown, 1983) and trait group selection (Wilson, 1980).

a) Kin selection

This is the most intuitive category of co-operation. Here one animal decides to cooperate with another only because the later is a blood kin of the former (Hamilton, 1964 a; b). The recognition of kin is achieved using different types of signals transmitted by the kin (olfactory, visual etc.; Griffiths, 2003). Hamilton (1964a;b) considers kinship based co-operation as a mechanism to enhance the fitness of the common genes that the co-operators bear among themselves. In many species the ability to recognize the kin is inherited (Neff and Sherman, 2005), but others achieve it by learning through experience (Griffiths, 2003).

Excellent examples for the kin-based co-operation come from the studies using cichlid fishes (Taborsky, 1984; 1985). In *Lamprdogous brichardi* sexually matured offspring stay at the nest and help the breeding parents to maintain and defend eggs (Taborsky, 1984; 1985). In another cichlid, *Neolampologus pulcher* (Brouwer *et al.* 2005; Bergmuller and Taborsky, 2005; Bergmuller *et al.* 2005) two types of helpers can be seen; smaller ones (younger) and larger (older) ones. According to Brouwer *et al.* (2005), smaller helpers, which cooperate more than the older helpers, are found to be more closely related to the breeding pair and brood. Atlantic salmon, which usually defends territory by attacking the intruders, may avoid the decision to fight and allow the intruder to share the resource, if the latter is a kin (Griffiths and Armstrong, 2000).

b) Reciprocity

In reciprocity (also mentioned as direct reciprocity, directed reciprocation or reciprocal altruism) an act of co-operation is repaid to the co-operator by the recipient at a future time (Dugatkin, 1997; Sachs *et al.* 2004). The decision of continuing the co-operation in this system is dependent upon the behaviour of the partners. If the partners behave honestly, the co-operation may continue. However, this type of co-operation decisions are under the shadow of cheating; after receiving the beneficial act from the co-operator, the recipient simply does not return the favour, as this strategy provides higher pay-off to the cheater. Hence, the defection from the side of any of the partners can lead to the termination of co-operation. This strategy of retaliating in the same coin is often referred to as ‘tit for tat’ (TFT ; Axelrod and Hamilton, 1981; Axelrod, 1984).

The reciprocity is highly dependent on the cognitive abilities, like individual recognition, memory of the features helping to recognize the co-operators etc. The ability of egg trading black hamlets (*Hypoplectrus nigricans*) to remember and continue egg trade with honest partners and avoid co-operation with cheaters (Fischer, 1980; 1981) is an excellent example for reciprocal altruism. Another illustration comes from the preference for the better co-operators during the predator inspection by three spined sticklebacks (Milinksi, 1987; discussed in detail in chapter 2 of section 1).

c) Byproduct mutualism

Byproduct mutualism is a form of co-operation during which two or more individuals decide and work together for achieving an outcome that could not have been achieved as efficiently (or not at all) by any single individual (West Eberhard, 1975; Brown,1983; Connor, 1995) and there is no temptation for either individual not to co-operate. This type of co-operation is also known as no cost co-operation (Dugatkin, 1997), pseudoreciprocity (Connor, 1986), selfish co-operation (Stevens and Hauster, 2004), and two way by products (Sachs *et al.*2004). Byproduct mutualism is a product of environmental situation which compels the animals to take co-operative decision in a harsh environment and to do not co-operate in mild environment. The co-operative hunting by moray eels (*Gymnothorax javanicus*) with two grouper species (red sea coral grouper, *Plectropomus pessuliferus* and lunar tail groupers, *Variola louti*) can be considered as an act of byproduct mutualism in fishes (Bshary, 2000). The groupers will attract the attention of eels by shaking their body and will lead eels to the site and recruit them to hunt the prey species hiding inside the corals. The groupers are taking the help of eels to flush out the prey species hiding inside the corals, an act impossible to the groupers. Here the eels and groupers are mutually benefited from the co-operative hunting and both species are rewarded with food for following a co-operative decision (Diamand and Shpigel, 1985).

d) Trait group selection

In this extreme level of co-operation, an individual of a group decides to self sacrifice for the well being of other group members (Willson, 1975). Even though, a highly criticized concept by the evolutionary biologists (William, 1966), Dugatkin and Mesterton – Gibbons (1996) argues that the presence of members decided to sacrifice for the group can enhance the fitness of a local group (often called trait group). Sober and

Wilson (1998) have demonstrated that the groups with self sacrificing co-operators are more productive than the groups without such co-operators. For instance, in guppy population, individuals dare to inspect predators to know their motivational status. This inspection behaviour, though deadly to the inspector, can be helpful to other group members as information about the predator is passed to the remaining group members for free. Dugatkin and Godin (1992 a) have demonstrated that the populations of guppies with inspectors are less often attacked by the predators than the groups with out inspectors. Besides, Dugatkin and Alfieri (2002) states that the group can enhance their productivity if the group members can segregate other members into cheaters and co-operators and remember the better co-operator while taking a decision to co-operate.

Individual decision and collective behaviours

A fish aggregation results when individuals decide to join a group (Pitcher and Parrish, 1993). Though all group members possess a common decision to join a group, each individual is provided with different levels of motivational status, learning ability and personality (Fernö *et al.* 2006). Hence, an individual fish will have to face a new situation composed of complex interactions of rigid and flexible components with new stimulus-response system in a group (Fernö *et al.* 2006). Additionally, in social situations, individual decision may not be valuable, as the individual cognitive control is lost and individuals are compelled to shift towards a group decision (either consensus or compelled decision) derived from the laws of emergent school structures and self organization (Camazine *et al.* 2001; Couzin *et al.* 2006).

According to Nøttesad *et al.* (2004) small changes in individual decision have a powerful impact on the emergent social decisions. If the outcome decision is not what the fish expected, a shift from high level ‘off line’ cognitive control to a low level ‘on line direct control’ (stimulus-response system) may occur, resulting in a chronic stereotyped behaviour and behavioural pathology. Hence, in such a context the individual decision may not be beneficial (either to the individual or to the shoal) and the fishes may find themselves trapped in collective maladaptive behaviours, which may negatively influence several vital biological processses like growth and reproduction. Consequently, individuals compromise with the situation by sacrificing individual decisions and will assemble into structured group with specific positions, to obtain the enhanced benefit of group life. This hypothesis was proven true in the case of salmons (Fernö *et al.* 1988) where two divisions of fishes have been observed to co-exist in salmon net pens, with fishes at the centre swimming in different directions and fishes along the net walls in a polarized school like way (Fernö *et al.* 1988; Juell, 1995). Overtime, the polarized group became larger and eventually took over the whole cage indicating that fishes prefer to join structured division to obtain the benefit of shoal life and adaptive collective behaviours can develop in an aggregation of fishes (Fernö *et al.* 1988).

The two individual characteristics which can impart its influence on the decision of a fish group are the boldness and social learning ability of members. The bold individuals are aggressive and always occupy the front position in a fish shoal due to their dominant nature. Being the occupants of the leading position in a shoal, their decision can influence the decision of the shoal in many contexts (Sundstrom *et al.* 2004). Social learning, a vital aspect of social life to obtain the benefits of group life, takes place when an individual fish learns to associate the behaviour of their shoal mates with reward or aversive events (Griffiths *et al.* 2004). Hence, during the social learning, the decision of somebody else is followed blindly, as it can reduce the cost of energy to be spent during the trials of decision making, execution and learning (Laland *et al.* 2003; Kelly and Magurran, 2003).

Conversely, the social learning can cause trouble to the learner if the demonstrator transmits the non-adaptive decision making tactics. Furthermore, in an environment were fishes are primarily influenced by the social stimulation and food (eg. culture pond), copying other fishes should strongly influence culturally mediated group behaviour with various unpredictable outcomes in species not adapted to a group life. In such contexts, appearance and maintenance of behavioural pathology and maladaptive decision making ability can affect the fidelity of structure and synchronization of activities in a shoal, ending up in the fitness loss of individual members comprising the shoal (Fernö *et al.* 2006).

Leadership and collative decision in a shoal

Though, a shoal behaves as a single organism in many occasions, the decision followed by a group may be originally taken by some members of the shoal. Usually in a shoal the majority of decisions are taken by the informed individuals (Swaney *et al.* 2001). As the decision making ability and the precision of a decision is correlated with the degree of information available, the naïve individuals of shoals cannot reach a decision as quickly as old members. Thus the naive fishes just follow the decision taken by another informed individual (Couzin *et al.* 2006), which is evident during the migration of pelagic fishes. During such migrations, movement of the fishes that have not previously performed any migration can be influenced by the decisions of experienced individuals. The extreme degree of this blind imitation can be seen during the migration of brown surgeon fish (*Acanthurus nigrofuscus*), where followers not only follow the route selected by the leader but also imitate their postural changes (e.g.; dip and rolls; Mazeroll and Montgomery, 1995).

Swaney *et al.* (2001) point out that the guiding ability of the informed individuals is correlated with their ‘knowledge’. Though, availability and the quality of information can enhance the precision of the decision taken by a group, the increase in the number of highly informed individuals can negatively affect the fidelity of a shoal as the heterogeneity in decision can lead to the splitting of a group into different subgroups (Couzin *et al.* 2006). When the number of informed individuals are very high, these individuals will become less willing to compromise and will leave the group often taking a sub set of individuals with them. Thus, Couzin *et al.* (2006) point out by quoting the subtle guide hypotheses, that the presence and percentage of informed individuals can influence the decision of naive individuals without requiring signalling and can guide group accurately. On the other hand, as the group size increases the required proportion of informed individuals needed to achieve a given accuracy decreases significantly.

The ability to make decisions, and how different factors influence the decision making in climbing perch in two conflicting situations: the binary choice situation, and in conflict for a single behaviour boldness has been discussed in two sections of this thesis. The section I deal with the effect of familiarity on decision making in different shoaling contexts and the section II discusses influence of various biologically significant environmental factors on the ability of climbing perch to take risky decisions.

Model System

The climbing perch

The model system used in the study was a commonly found freshwater fish *Anabas testudineus* (Fig.1). This fish is popularly known as 'climbing perch or climbing gouramy'. The common name 'climbing perch' originated from the legend that *A. testudineus* climbs coconut palms to suck juice. Probably the origin of this myth might have been from the observation that occasionally this fish is seen on coconut treetops during the rainy season. It is possible that birds like crows pick up the fish and place it on coconut trees as it travels over land during the monsoon (Norman, 1975). Climbing perch exhibits 'walking' on the land during rainy season and travels through the moist land by wriggling movements.

It is an obligatory air breathing fish which comes to the water surface intermittently for gulping the atmospheric air. The accessory respiratory organs seen inside of the operculum allows the animal to tide over drought if the air breathing organs are kept moist. During dry seasons, it lives buried in the mud and aestivates like the African lung fish (Thiraphan, 1984). The accessory respiratory system includes, labyrinthine organ and the respiratory membrane covering the supra branchial chamber (Bersa, 1997).

The other common names of the fish include Koi fish, Kawai and Kobhai (Bersa, 1997). In Kerala, it is known in different local names like Kalluthi, Karuppidy, Karuvathy, Kalladamutty, Kallemutty, Undeollee, Karup, Kallurutty, Karikanny, Kaithakkora, Karatty, Porukku etc.

Distribution

This fish is common in the fresh water bodies of South and South East Asia (Yakupitiyage *et.al.* 1998). In South East Asian countries, it is found in India, Pakistan, Nepal, Bangladesh, Sri Lanka, Burma, Thailand, Indonesia, Singapore, Philippines, and China. In India it is common in the northern states like Bihar, West-Bengal, Orissa, Uttar Pradesh (Bersa, 1997) and southern states like Kerala, Karnataka, Andhra Pradesh and Tamil Nadu.

Systematics

Phylum	:	Vertebrata
Sub-phylum	:	Craniata
Super class	:	Gnathostomata
Series	:	Pisces
Class	:	Teleostomi
Sub class	:	Actinopterygii
Order	:	Perciformes
Family	:	Anabantidae
Genus	:	*Anabas*
Species	:	*testudineus*

Diagnosis

D XVI-XVIII, 8-10; A VIII-XI, 9-11; Pi, 13-14; V 15 (Talwar and Jhingran, 1991)

The fish has a posteriorly compressed long body with rather broad head. The shape of the body of the fish varies with age, habitat quality and food items consumed. It is olive green to dark brown along the dorsal side and very pale in colour below, with golden red eyes. Young fish have transverse dark stripes on the hind part of the body and tail and a similar longitudinal stripe running from the eye to the operculum (Yakupitiyage *et al*. 1998). Young fishes also have a large dark spot at the base on either side of the caudal fin and a small spot at hind boarders of the operculum (Yakupitiyage *et al.* 1998). In adults the stripes disappear and the black blotches are often lacking.

Mouth is terminal and relatively large with upper jaw weakly producible. Jaws are provided with villiform teeth. The gill covers are serrated and unlike other teleosts the opercula and subopercular bones are not fused into a single operculum, instead a thin flexible membrane binds them, so that the fish has two sections of the gill cover hinged separately: the opercular on the suspensorium and the subopercular on the rear part of the lower jaw. The gill cover open very widely and the sub opercular rotate vertically as well as laterally. Scales are large and ctenoid type and regularly arranged. Two lateral lines in 21-29 scales are present. Dorsal and anal fins are long and composed of strong spines and soft fin rays. Dorsal fin with 16-18 strong spines and 8-10 soft rays. Pectoral fins are bluntly rounded. Pelvic fins are with one spine and five soft rays. Caudal fin is also rounded. Dorsal and caudal fins are grey, pectoral and anal fins are pale yellow and pelvic fin is pale orange in colour.

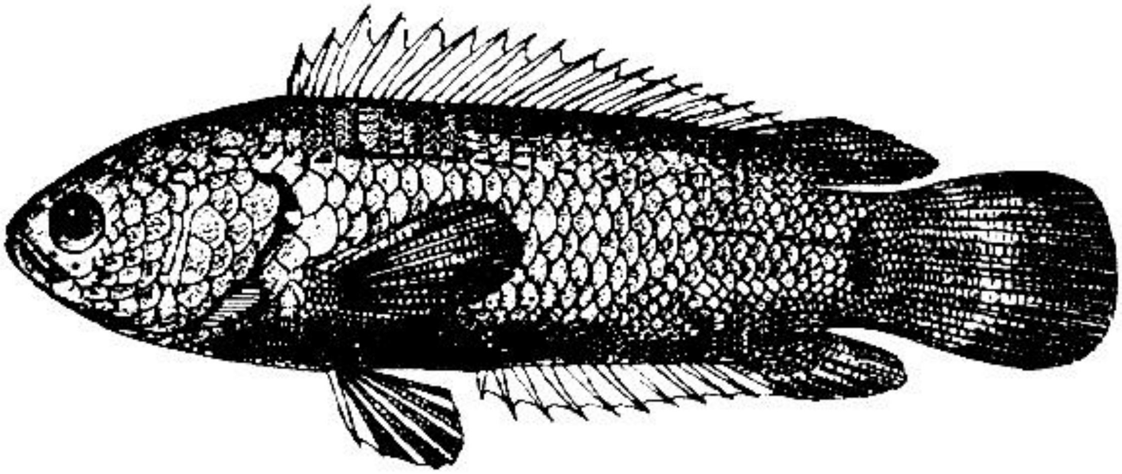


Figure 1. Climbing perch (*Anabas testudineus).*

Habit and habitat

This fish inhabits water bodies like ponds, lakes, paddy fields, flooded fields, stagnant water bodies and sluggish flowing canals. Climbing perch can tolerate extremely unfavourable conditions and is seen in sewage canals and hydrogen sulphide rich pools with fowl smelling murky water. They can tolerate salinity and is found in brackish water and areas where seawater intrusion occurs. Adult climbing perch is omnivorous in habit. Larvae and young fry feed on phytoplankton and zooplankton. Fingerlings and adults feed on crustaceans, worms, molluscs, insects, algae, soft parts of aquatic plants and organic debris (Prasanth, 2005).

Section I

Familiarity and shoaling decisions

Familiarity and fish decisions

The experience with objects or individuals leads to the development of familiarity in animal species ranging from invertebrates to advanced vertebrate like *Homo sapiens*. Familiarity is defined as a personal knowledge or information about someone or something, and familiarization leads to recognition of something or someone by remembering the past experience (D K Illustrated Oxford Dictionary, 1998). The ability to acquire familiarity with conspecifics or heterospecifics is reported in a wide taxa of animals (mammals: Porter *et al.* 2001, Birds: Wiley *et al.* 1999; Cristol, 1995; reptiles: Bull *et al.* 2000; insects Clark, *et al.* 1995).

The familiarity can influence the decision making ability of fish in many contexts (Barber and Wright, 2001; Binoy and Thomas, 2004). In recent years, it has become evident that fish can discriminate familiar conspecifics or heterospecifics from unfamiliar counterparts and behave differentially in familiar and unfamiliar habitats (Brown, 2001; Griffiths, 2003). There is considerable body of evidence to show that large number of fish species recognize and preferentially associate with familiar school/ shoal mates or neighbouring territory holders (Griffiths, 2003; Krause, *et al*. 2000). Moreover, given a choice between familiar heterospecifics and unfamiliar conspecifics, fish prefered to associate with unfamiliar heterospecifics, highlighting the overriding influence of familiarity on decision of joining a shoal of conspecifics (Ward *et al.*, 2003).

Acquisition and fading of familiarity

Acquisition of familiarity

Familiarization is a time dependent process that takes place through continuous interaction, with conspecifics, heterospecifics or habitat cues. The time required for the acquisition of familiarity varies from species to species (O' Connor, 2000). For example, a small group of guppies (6 in number) took 14 days to develop familiarity with each other (Griffiths and Magurran, 1997). A study using threespined sticklebacks revealed a gradual increase in familiarity over a four week period of association (Magurran *et al.* 1994). By contrast, Ward *et al.* (2005) have shown that the threespined sticklebacks require only 24 hours' experience with other fish for the development of familiarity. Using co-operation during predator inspection as assay in stickleback model, Milinski (1987;1990) demonstrated that these fishes required only four trials of predator insepction with a conspecifics to develop familiarity. Moreover, Dugatkin and Alfieri (1991) repeated the same experiment using guppies and reported that this species require only the experience of less than four minutes to develop familiarity and to select a familiar partner during the predator inspection.

Fading of familiarity

Fading of familiarity is a gradual process, very similar to the familiarity acquisition process (Utne-Pam (2001). Her works revealed that brown trout, which acquired familiarity with conspecifics, gradually lost their acquaintance within 4 weeks of isolation. By contrast, rainbow trout (*Onchorynchous mykiss)* was able to forget their territorial combatant after a separation period of 72 hours (Johnsson, 1997). Fading of familiarity is important because under certain circumstances memory decay can also be adaptive, as forgetting the social status may help the fish to regain its dominant status in another contest after the familiarity has been faded (Miklosi, *et al.* 1992; Warburton, 2003). However, European minnows remembered their familiar conspecifics even living in isolation for six months (Bhat and Magurran, 2006).

Gender difference in the familiarity based decisions

In fishes the ability for acquisition of familiarity and decision making based on familiarity shows gender specificity. Females are more efficient in the acquisition of familiarity and exhibit preference for the same sex familiars (Griffiths and Magurran, 1998; Croft *et al.* 2004; 2003). Female guppies, which spent a greater proportion of their time in a shoal, developed familiarity and enjoyed greater benefits of shoaling than males (Croft *et al.* 2004).

The male fishes are likely to recognize familiars, but behave differently towards them only in the context of mate choice (Kelly *et al.* 1999). The reason for this sex specific variation in the familiarity dependent behaviour may be the difference in strategies used by two sexes to enhance their fitness. As far as male fish is concerned, investing time and energy for gaining familiarity will be an extra cost as they devote much of their time seeking mating opportunities (Griffiths, 2003).

Social status and familiarity

Recent researches demonstrate that social status influence decision making capacity in the juveniles of angel fish (*Pterophyllum scalare* ; Gomez- Laplaza and

Fuente, 2007). Here, the subordinate fish showed a preferential association with familiar subordinates over unfamiliar subordinates, but preferred the unfamiliar shoal over the familiar one when both shoals constituted of dominant individuals. The shoaling behaviour shown by the dominant fish, on the other hand, indicated no significant preference for any of the shoals regardless of their composition. Results of this study also suggest that fishes are able to differentiate between different stimulus shoals and demonstrate that the pervasive influence of familiarity on the shoaling decision may be restrained or overridden by the composition of the familiar shoals and the social status of the test fish (Gomez- Laplaza and Fuente, 2007).

Familiarity is context dependent

Similar to many other behaviour patterns, decisions based on the familiarity is also context dependent. Hence, it could the suggested that the fish trade-off many factors, while taking a decision based on familiarity. According to Day (1999), the individuals of rainbow fish were able to become familiar with two shoals in two separate contexts (feeding and predation). In later trials, when given a choice between both familiar shoals, they showed varying preferences that correlated with the context in test situations.

The kin

Many species of fishes have the ability to recognize and behave differently towards the individuals with which they have blood relation i.e., the kin (Ward and Hart, 2003). In many species, kin based behaviours vary in accordance with the degree of relatedness. For instance, when females of rainbow fish were presented with male conspecifics, the preference followed the order of non kin<half sib<sib, while taking a mate choice decision (Arnold, 2000). The preference for for related conspecifics has been especially well described in the juveniles of territorial anadromous species such as Atlantic salmon (*Salmo salar,* Brown and Brown, 1992; Moore *et al.* 1994); Coho salmon (*Oncorhynchus kisucth,* Quinn and Busack, 1985); Arctic charr (*Salvelinus alpinus*; Olŝen, 1989; Winberg and Olŝen 1992; Olŝen *et al*. 1998) and rainbow trout (*Oncorhychus mykiss* Salmonidae; Brown and Brown 1992).

Overlapping kin recognition and familiarity

The relation between kin recognition and familiarity has been analyzed in the light of life history traits in many fish species (Ward and Hart, 2003). This is because the selection pressure on the recognition system is different on the parental nest building species and the egg scattering pelagic spawners. In nesting species, fishes get a chance to develop templates for both kin and conspecific recognition, as siblings (kin) are the first conspecifics encountered (Grafen, 1990). Such species can depend on familiarity as a base for recognition and a separate complex mechanism for kin recognition is unnecessary (Blaustein and O'Hara, 1986). The development of dual template system is not possible in egg-scattering pelagic species, as there is no surety that the conspecifics with which they develop would be a kin.

Many species use both kinship and familiarity as criteria for assessment of potential shoal mates (e.g. rainbow fish, *Melanotaenia sp.*). There is sex specific variation in the usage of familiarity and kin recognition while selecting a shoal, due to the dissimilarity in the selection pressure experienced by males and females. For example, female guppies utilize familiarity over kinship while taking a shoaling decision (Kelley, *et al.* 1999).

In many contexts, behaviour towards a kin is almost similar to that expressed towards a familiar individual (Grifffiths, 2003). Hence, many authors believe that in species exhibiting kin recognition, the recognition template (the internal representation of such characteristics used to distinguish the kin) is inherited (Grosberg and Quinn, 1986; Neff and Sherman, 2005). The template formation is dependent on morphological (Tibbetts, 2002), vocal (Harre, 1998) and chemical (Todrank and Heth, 2003; Mateo, 2002) cues, which may vary from species to species. Moreover, this ability to recognize a kin and to engage in kin-selected behaviour (Ward and Hart, 2003) forms the basis of several vital decisions in the life history of individuals or social groups and improves the fitness of the fish through the resultant benefits of inclusive fitness.

Neff and Sherman (2005), using blue gill sunfish (*Lepomius macrochirus*), demonstrated that the males of this species are able to recognize their offspring from the young ones of alien males, even if they have no prior experience with them. Here, fathers were able to recognize their offspring born and brought up in the laboratory after *in vitro* fertilization and reared in separate tanks without any sort of contac,t using the odour cues emitted by the young ones (Neff and Sherman, 2005). These authors concluded that males of blue gill sunfish are using their own odour, a genetically determined factor, as the referent phenotype to match with that of the offspring, while recognizing them.

Though, the hypothesis put forward by Neff and Sherman (2005) gives more emphasis to the genetic determination of kin recognition and support the idea that fish has an internal representation of kin odour, development of familiarity through social learning is also well documented in fishes (Engezer *et al*. 2004, Winberg and Olsen, 1992). Guppies show an active preference for swordtails (*Xiphophorus helleri)*, when juveniles of the former species were raised with the latter, which indicate that familiarity has a significant role in recognition (Warburton and Lees, 1996). In an experiment designed to investigate the strength of kinship and familiarity in guppies, Giffiths and Magurran (1999) describe that this fishes opted shoal mates on the basis of familiarity rather than kinship. Additionally, studies using Atlantic salmon have shown that that isolation from the egg stage makes the fish unable to recognize their conspecifics due to the underdevelopment of templates resulting from the lack of social stimuli (Olsen and Winberg, 1996).

Many studies have demonstrated that the major histocompatibility complex (M.H.C) based odorants produced by an individual fish and transported by water currents are acting as the base for discrimination of kin from non-kin (Olsen *et al.* 1998). Kin recognition based on olfactory cues has been demonstrated in Arctic charr (*Salvelinus alpinus,* Olsen, *et al.* 1998), Coho salmon (*Onchorhynchus kisutch*, Quinn and Hara, 1986); Atlantic salmon (*Salmo salar*) and rainbow trout (*Onchorhynchus mykiss;* Brown *et al.* 1993). However, juveniles of stickleback (*Gastrosteus aculeatus*) preferred to associate with siblings over non-siblings when provided olfactory cues in combination with visual stimuli (VanHavre and Fitzgerald, 1988).

Arnold (2000) has demonstrated that preference of female rainbow fish to the kin largely depends on the context. Here, the females showed associational preference to full sibling over half-sibs, and preferred both over non-kin female conspecifics. However, in a mate choice situation the females preferred non-kin males over full or half sibs, indicating the potential ability to realize the kin association in social context, and avoidance behaviour in terms of the probable inbreeding (Ward and Hart, 2003).

However, in spite of clear kin preference and potential inclusive fitness advantage afforded by kin selection theory (Hamilton, 1964a;b), there is little evidence for kin based association patterns observed in the wild, either among territorial fishes like brown trout (Carlsson and Carlsson, 2002) or among schooling fishes like common shiners (*Notropis cornutus*, Ferguson and Noakes, 1980), and coral reef fish (*Anthia squamipinni,* Avise and Sharpio, 1986). The possible explanation for this observed discrepancy between laboratory studies and field observations is the common rearing of family groups in the laboratory leading to kin recognition, whereas, in natural streams and rivers familiarity rarely develops among relatives due to dispersal of the population and other factors (Griffiths, 2003). For instance, Arctic charr reared in isolation from egg stage do not discriminate kin from non-kin (Winberg and Olsén, 1992; Olsén and Winberg, 1996), suggesting that the recognition template by which fish discriminate siblings from unrelated individuals is probably learned.

Familiarity and foraging

Familiarity modifies selection of foraging tactics and decisions in fish. Brown and Day (2002) argue that the familiarity with different food item is an unavoidable factor for the development of a menu and foraging skills in fishes. Fishes that have no wide range of experience with various food items will hesitate to test a novel food item or to take a decision to modify the food handling strategies to cope with the novel prey. However, during the social learning of foraging tactics naïve fishes are seen to learn more from the demonstrator, if the latter is a familiar individual, perhaps because the fish may attend more closely to the behaviour of familiar individual than an unfamiliar conspecific (Griffiths, 2003).

The sticklebacks were faster in finding food and exhibited very high rate of food intake in presence of familiar conspecifics (Ward and Hart, 2003). Similarly, guppies explored new areas when accompanied by a familiar partner than with an unfamiliar partner (Bhat and Magurran, 2006). The familiarity between group members not only reduces the aggression for the control of food source but also improves the distribution of information among the group members (Griffiths, 2003). Swaney *et al.* (2001) found that guppies learned foraging task more rapidly from familiar conspecifics than from unfamiliar conspecifics, suggesting that socially learned skills spread rapidly through familiar sub-groups.

Familiarity can modify the decision taken during starvation, a condition where no distractions can affect the behaviour of a fish (Jain and Sahai, 1987). Sticklebacks (of all age group) which exhibit preference for the familiar group in all non sexual contexts shifted its preference towards unfamiliar shoals, when the test fish was hungry (Frommen *et al.* 2007). This result suggests that sticklebacks avoid competition with familiar conspecifics during the foraging situations.

Familiarity and the escape decision

Familiarization with threat stimuli plays a crucial role in the development and execution of antipredator responses in fish (Kelley and Magurran, 2003). Predator-prey interactions consist of three stages: detection, recognition and assessment, and attack avoidance. In other words, the initial detection of a predator is followed by recognition and assessment of the nature of the predator and likelihood of its attack. Familiarity with the predator as well as the tactics employed by the predator is essential for a fish to make a choice of appropriate antipredator behaviour. It has been assumed that antipredator behaviour is more genetically determined than most other aspects of behaviour. Many species of fish do not require experience in order to recognize and respond to visual cues emitted by their natural predators (Kelly and Magurran, 2003). For example, predator naïve paradise fish (*Macropodus opercularis*, Anabantidae) show a stronger reaction towards sympatric than to allopatric predators (Gerlai, 1993) and humbug damselfish (*Dascyllus aruanus*) can distinguish between piscivorous and nonpiscivorous heterospecifics (Coates, 1980). This conclusion is reinforced by the observation that populations subjected to varying levels of predation risk in the wild continue to express their characteristic patterns of antipredator behaviour when reared under standard conditions in the laboratory (Kelley and Magurran, 2003).

However, recent literature shows that fish can make subtle and adaptive changes in their antipredator behaviour repertoire through learning and experience. Studies by Griffiths *et al.* (2004) demonstrated that juvenile brown trout (*Salmo trutta*) reacted more quickly to a simulated predator attack and gathered more food items in a group of familiars than when in a group of unfamiliar fishes. Experience and familiarity plays an important role in the recognition of predator using odour cues (Magurran, 1989; Chivers and Smith, 1998). Utne-Palm (2001) demonstrated that predator naïve two spotted gobies (*Gobiusculus flavescens*) avoided areas in which they encountered an Atlantic cod (*Gadus mohrua*) predator, but failed to avoid habitat with odour of cod. However, following exposure to a live cod in association with odour cues, gobies showed strong avoidance of cod odour. It is suggested that the gobies are predisposed to display an avoidance response towards visual cues of predators, but recognition of olfactory cues requires familiarity. Only three consecutive exposures to the predator odour were enough for the development of familiarity with the odour of the cod (Utne-Palm, 2001).

Attack unfamiliar - avoid familiar

Familiarity is negatively correlated with aggression. In shoaling fishes, familiarity with shoal mates increases shoal cohesion and reduce aggression. Improved shoal cohesion will enhance the benefits of shoal living by augmentation of the performance of synchronized activities. Similarly, territorial fish can increase its foraging time by diverting more energy and time used in aggression for other activities, if it can develop familiarity with its neighbours (Griffiths, 2003). The reduction of aggression due to familiarity with conspecifics is reported in brown trout. They settle their territorial disputes and avoid escalation of fights if they have previous experience with one another (Johnsson, 1997; Johnsson and Åkerman, 1998). This result indicate that familiarity helps to maintain a more stable system of hierarchy among individuals which in turn will reduce the energy invested in aggression to establish dominant status in each encounter (Switzer *et al*. 2001).

The dominance status developed among the individual fishes is less susceptible to status reversal (Switzer *et al.* 2001). However, the benefits of reduced aggression level may only be maintained by reaffirmation of familiarity status. In a study, Johnsson (1997) found that the separation of pairs of territorial combatants for a period of three days was sufficient for the decay of familiarity dependent aggression reduction.

Familiarity and mate choice

Remembering and recognizing mate can help the fish to avoid repeated mating with the same mates. Male Trinidadian guppies show clear preference for unfamiliar females (Griffiths and Magurran, 1998), perhaps for maximizing their reproductive success (Kelly *et al.* 1999). Similarly, male Panamanian bishop fish (*Brachyraphis episcopi*) use familiarity to avoid mating repeatedly with the same subset of females, both in laboratory and field trials (Simcox *et al.* 2005). Hermaphroditic fish, black hamlet (*Hypoplectrus nigricans*) always preferred familiar and dependable partners for egg trading. In a mate choice situation, female rainbow fish selected male conspecifics in the order, non kin<half sib<sib. This study indicates that female rainbow fish is able to realize the benefits of kin association in group formation and the disadvantages of association with kin in the context of breeding.

Familiarity with the environment

Familiarity with spatial properties (distribution and specific location of objects, obstacles and profitable resources like food patches) of the habitat can influence various types of decisions taken by a fish. Thorough experience with the spatial properties helps the fish to exploit site specific resources more successfully and to select escape routes quickly, as the decision maker knows well about position of shelters and hiding places (Jordan *et al.* 1997; Brown, 2003). For instance, familiarity with the habitat influence the escape behaviour of the crimson spotted rainbow fish (*Melanotaenia duboulayi*), where individuals familiar with physical charecteristics of the habitat make more successful escape response during a predator attack (Brown, 2001).

The familiarity with spatial properties can also help the fish to regain its territories after a temporary displacement by natural forces or due to anthoropogenic activity like fishing (Mathews, 1990). For instance, black and yellow rock fish (*Sebastes chrysomelas*) when displaced from their territories, those individuals which were more familiar with the territory located and regained the site earlier than those fish which were not so familiar with the territories (Hallacher, 1984).

A classic demonstration of the influence of familiarity with the spatial properties of the environment on the decision making ability of a fish is illustated in experiments using Gobid fish (*Ballygobius soporator*; Aronson, 1951;1971). When threatened, these gobies jump from their home tide pool to an adjacent pool with impressive accuracy. Aronson (1971) noted that only those fishes that were acquired familiarity with the spatial distribution of the pools at high tied were able to take a successful decision of jumping into an appropriate pool during the simulated attack in low tide.

Socio-environmental correlates of familiarity

There is a wide spread belief among fish behaviour researchers that familiarity is correlated with habitat quality and population density (Griffiths, 2003; Ward *et al.* 2002b; Hilborn, 1991). Griffiths (2003) supports this assumption and points out that as habitat complexity and the number of conspecifics encountered increases, the chance for getting acquainted at least with a few conspecifics decreases due the increased difficulty of individual fishes to discriminate familiar from unfamiliar conspecifics. Hence, in such large shoals the development of familiarity is constrained and individual fish faces difficulties in discriminating familiar from unfamiliar. Moreover, Ward *et al.* (2002b) suggest that due to the enhanced familiarity, small sub shoals may remain together for extended periods. This hypothesis was tested by authors like Mapston and Fowler (1998), Hoare *et al.* (2000), Ward *et al*. (2002b) etc. Mapstone and Fowler (1998) discovered that group membership was more stable among coral fishes, which typically show a high degree of site fidelity that promote high levels of local familiarity. Meanwhile, resident species of shallow freshwater habitats involve in a more flexible familiarity based relationship.

Familiarity in laboratory and in field

The acquisition of familiarity as well as its impact on decision making have been reported in many species of fishes like bluegill sunfish (*Lepomes macrochirus*, Miklosi *et al.* 1992), guppies (Magurran *et al.* 1994), fathead minnows (Brown and Smith, 1999), chub (*Leuciscus leuciscus*, Ward and Hart, 2003), when tested in the laboratory.. Klimley and Holloway (1999) monitored 38 electronically tagged yellowfin tuna (*Thunnus albacarcs)* found repeated reoccurrence of particular pairs or groups of individuals at particular site. An exhaustive study conducted over a period of 14 years, involving tagging of 570000 individual Pacific herring (*Clupea pallasi*) concluded that individuals formed associations that persisted for a period of several years and over considerable distance (Hay and Mc Kinnel, 2002). The species like sticklebacks (Barbar and Ruxton, 2000) yellow perch (*Perca flavescence*, Helfman, 1984), steelhead trout (*Onchorhynchus mykiss*) etc. have also been reported to show familiarity dependent variation in decision making in the field.

Sticklebacks exhibit ability for the acquisition of familiarity with other individuals in field and laboratory, whereas some other species that exhibit familiarity dependent behaviour in the laboratory condition failed to show such behaviours in the field (Griffiths, 2003). The inconsistency between laboratory observations and field data may be originating from difference in population density and habitat complexity in each condition. In the laboratory, population density is low and complexity of the environment is less, hence the chance to encounter and to interact with the group members is more. Additionally, due to the large number of individuals present, shoals exhibit lesser levels of fidelity in field (Griffiths, 2003)

Familiarity and recognition: application in aquaculture and conservation

Sharp decline in the number and population size of many fish species, including commercially important ones, are a major problem faced by fisheries managers and conservation biologists. The way in which relatedness and familiarity mediate interactions suggests application of the results of this research in culturing commercially important species and in restocking and reintroduction of critically endangered species in their natural habitats (Ward and Hart, 2003, Brown and Day, 2002). Many studies show that relatedness and recognition can affect population density and growth. For example, Greenberg *et al.* (2002) found enhanced growth rate of juvenile brown trout when reared as a mixture of siblings and non siblings compared to a single family group in large enclosures. The study conducted by Griffiths and Amstrong (2001) shows that in Atlantic salmon the density was almost double in the populations with non kin individuals than in population composed of close relatives.

Höjesjö *et al.* (1998) reported that familiarity stabilized dominance hierarchies and generally reduced the number of aggressive interactions between fishes. Juvenile Atlantic salmon (*Salmo salar*, Salmonidae) signal their submissiveness to familiar dominant individuals by darkening their body colouration, thereby incurring less direct aggression (O'Connor *et al.* 2000). Similarly, the ability of rainbow trout to recognize individuals allows third-party observers to gauge the competitive ability of a pair of combatants by watching contests i.e., eavesdropping (Peake and McGregor, 2004). The observer fish may then use this information to assess its own chances of prevailing against either of the two fighters in any subsequent contest (Johnsson and Åkerman, 1998). Arctic charr (*Salvelinus alpinus*) that were maintained in familiar conspecific groups showed increased survivorship and better overall body condition than those maintained in non-familiar groups over a 21-days period, perhaps, as a consequence of stabilised dominance (Seppä *et al.* 2001). All these results remind that the understanding the basis of familiarity in fishes is essential for reducing mortality rate and to enhance the growth in culture ponds as well as in designing restocking protocol for the conservation of endangered and threatened fish species

Chapter I

Influence of familiarity on shoaling decision of climbing perch

INTRODUCTION

Fishes are strikingly social organisms; it has been estimated that more than 25 percent of the approximately 27000 species of teleosts form social groups throughout their lives and over 50 percent school as juveniles (Shaw, 1978). The term shoal refers to any social aggregation of fish, while schools are polarized groups showing synchronized swimming behaviour (Pitcher and Parrish, 1993). This social aggregation could either be mono-specific or multi-specific with various levels of rigidity. For example, fish associate for longer periods in tropical coral reefs and the association found in shallow water ecosystems is short-lived due to the highly dynamic nature of the shoals and the restriction in the space available for exploration (Hoare and Krause, 2003). However densely packed shoals with millions of individuals are formed by a number of species in the marine ecosystem (Hoare and Krause, 2003).

The phenomenon of exchange of individuals between shoals makes it complex and dynamic (Krause *et al.* 2000). There are evidence for the merging of shoal and exchange of individuals when two shoals meet the natural ecosystems. According to Croft *et al.*, (2003) shoals of banded killi fish show an encounter frequency of 1.1 minutes so that killi fish that were initially found together in the same shoal can be seen distributed over other shoals during the same day itself. By contrast, shoals of guppies encounter once in every fourteen seconds (Croft *et al.* 2003). However, many species of fish residing in coral reef ecosystems usually exhibit higher levels of shoal fidelity and reduced tendency to leave the shoal. (Krause *et al.* 2000) speculates that this fission - fusion system of shoal dynamics is beneficial to the individual fish as the migration of individuals from one shoal to another improves the individual benefits by exchange of information by social learning.

In nature, there are several situations when the fish may have to take an active decision either to desert or to join a shoal (Pitcher and Parrish, 1993). The shoals can break during the predator attack or due to anthropogenic activities like fishing. Additionally, in many fish species the shoals get dispersed during night when the fishes take rest and individuals re-unite to form a new shoal in the morning (Ryer and Olla, 1998).

A shoal is formed as a result of active decisions by some individuals to live together in order to get more benefit and fitness than when they are alone. Hence, fishes promote the enhancement of shoal size up to an optimum number, above which the cost of group living will override the benefit obtained from shoaling (Pitcher and Parrish, 1993). The fish actively estimate the costs of joining a shoal or decide to leave and join another shoal, if the benefit obtained from the former is very low compared to the latter. The benefits of shoaling include:

1. Increased foraging rate and success

According to Pitcher *et al.* (1982), fishes foraging in shoals gain benefits through faster detection of food, getting more time for feeding, more effective sampling, information transfer and opportunity for copying. In minnows, gold fish and stone loach

(*Nemacheilus barbatulus*, Street and Hart, 1985), faster location of patchy food in larger shoals have been experimentally demonstrated.

2. Enhanced protection from predators

Unlike solitary existence, shoal life provides enhanced protection from predators. The ways in which the fish shoals may counter attacks of predator could be included in the following logical categories; avoidance, dilution, abatement, evasion, detection, mitigation, inspection, inhibition and confusion (Pitcher and Parrish, 1993).

3. Increased hydrodynamic advantages

Fishes moving in shoals with three dimension shape are said to have getting hydrodynamic advantages (Weihs, 1973; 1975). In 1970, Zuyev and Belyayev demonstrated that 30 *Trachurus* cruising in a flume exhibited tail beat frequencies proportional to the distance from the front of the group. This result gives evidence for the hypothesis that fish in front had to work harder. Moreover, same authors point out that fishes moving in a shoal obtained hydrodynamic benefits from the group movement and use lesser amount of oxygen during the locomotion. The drag reduction resulting from the mucus produced by the members of a moving shoal is also attributed to the hydrodynamic advantage. However, Pitcher and Parrish (1993) noted that, though there are many theories and hypothesis available to explain the question why fishes inhabiting natural habitat move in a three dimensionally structured shoal, none of them explain doubtlessly the mechanism of hydrodynamic advantage. Hence, there is further scope for a more comprehensive theory to explain the phenomenon.

The cost of shoal life

The major cost of shoal life is the increased competition and aggression as large number of animals in a group is trying to get control over the same resource. Another cost is the greater possibilities of transmission of parasites and pathogens due to the aggregation of large number of individuals in a small area (Pitcher and Parrish, 1993).

Factors influencing shoaling decision

A number of other factors influence the shoaling decision of a fish. Analysis of the literature reveals that different species of fishes use different criteria and cues to reach a shoaling decision (Hoare and Karuse, 2003). The major factors affecting the shoaling decision of a fish are:

a) Species

Many species of fishes show an active preference for shoaling with conspecifics. For example, brown trout (Brown *et al*. 1993) and banded killi fish (Krause and Godin, 1996). Shoaling with the members of the same species is highly beneficial as all members possess similarity in the morphology, which provides better predator avoidance by reducing the oddity and enhancing the dilution effect (Hoare and Krause, 2003). Moreover, the members of monospecific shoals can enjoy higher degree of synchronization in their behaviour due to similarities in the strategies employed for the fulfilment of their needs.

b) Size

According to Griffiths (2003) individuals of many species prefer to join a shoal of conspecifics having identical size. This preference for shoals comprised of the individuals with matching size is not restricted to conspecifics. There are reports stating that many similar sized individuals of different species join together to form a multi specific shoal, when the conspecifics are not readily available. For example, fishes living in subtropical and tropical reefs are usually found in heterospecific shoals (Overholtzer and Motta, 2002).

c*) Sex*

Sex of the shoal members can influence the decision of individuals while joining or deserting a shoal. Poeciliid fishes are also shown to consider the size of the individuals of the opposite sex in the context of shoaling decision (Marler and Ryan, 1997, Whitte and Ryan, 1998). By contrast, Gabor (1999) has reported that preference for larger individuals were common, regardless of sex of the shoal mates in sailfin mollies.

d) Physical status

Fishes usually prefer to join a shoal of individuals with matching abilities, because effective group performance like escape response from predators is possible only when all members of the group have comparable swimming ability. Additionally, the hydrodynamic advantage obtained while moving in a group will be very high, if all the members have almost similar swimming potential (Pitcher and Parrish, 1993).

e) Parasites and diseases

Parasitic infection and other diseases reduce the swimming ability of the fish making it more vulnerable to predator attack. The infected fishes get passively assorted into a new group, as they are unable to swim along with the major group (Guthrie and Kroger, 1974). Hence, a fish desirous of joining a shoal do so, after assessing the prevalence of parasitic infection and parasitic load of the target shoal (Hoare *et al.* 2000).

f) Competitive ability

Many species of fishes prefer to shoal with individuals having lesser competitive ability. This strategy of shoaling with poor competitors reduces cost of intraspecific competition (Metcalfe and Thomson, 1995).

g) Number

Most of the fish species studied prefer to join shoals composed of larger number of individuals as this strategy provides more benefits like dilution effect, early detection of predator or food etc. **(**Reebs and Saulnier, 1997; Lachlan, *et al.* 1998).

Familiarity and shoaling decision

Familiarity is an important factor that affects shoaling decision of a fish. Certain species of fish prefer to join a group composed of familiar conspecifics to those composed of members that they have not encountered previously (Magurran *et al.* 1994; Griffiths and Magurran, 1999). The development of familiarity is time-dependent and a long-lasting phenomenon (Griffiths and Magurran, 1999). It has been shown that familiar individuals may even re-assort after enforced mixing with non-familiar individuals (Barber and Ruxton, 2000). However, the strength of familiarity as a shoal cohesion force has not been fully understood yet (Binoy and Thomas, 2004; Barber and Wright, 2001). Hence, two important studies assessing the effect of familiarity on shoaling decision of climbing perch are presented in this chapter.

a. Whether climbing perch posses the ability to acquire familiarity with its conspecifics?

b. How strong is the influence of familiarity on the shoaling decision of the species?

MATERIALS AND METHODS

To analyze the shoal size preference and the effect of familiarity on group shoaling decision, climbing perches (standard length 6 ± 2 (SE) cm) were collected from ponds of Irinjalakuda (10˚ 25’, 10˚ 18’47’’ N Latitude and 76˚ 17’19’’, 76˚ 12’ 48’’ E Longitude), Thrissur district, Kerala state, India, during February-April 2002 and transferred to the laboratory. They were kept in groups of twenty in glass tanks (120 cm × 60 cm × 60 cm) for 14 days to make them familiar with each other. The tanks were filled with pond water up to 40 cm and provided with a sand substratum. Artificial food pellets (Marvel feeds, manufactured by Aquarium Systems, India) were given to the fishes twice daily.

It has been observed that acclimation is one of the major factors that influence performance in preference tests (Bateson, 2004). The fish moved freely and showed normal behavioural patterns only after getting experience of five minutes for four cosecutive days with the experimental set-up. Hence, all test fishes were acclimatised individually with the experimental arena in the absence of stimulus shoals. The data thus obtained have not been considered for analysis.

Apparatus

Experiments were conducted in a 70-litre aquarium (85 x 32 x 32 cm), which was divided into three chambers; two side chambers (16 x 32 x 32 cm each) and a central chamber (53x32x32 cm, Fig.1). The partitions were made of perforated transparent acrylic sheets. Three sides of the aquarium were covered using black paper. The test fish was always introduced individually into the central arena in a presentation cage made of transparent perforated acrylic sheets (15x 10x 27 cm) with a sliding door on the top. The bottom of the presentation cage was open so that the test fishes can be released in to the experimental arena by raising it. The water level in the set-up was 28 cm. A compact fluorescent lamp (11 w) was lighted on the top of the set-up.

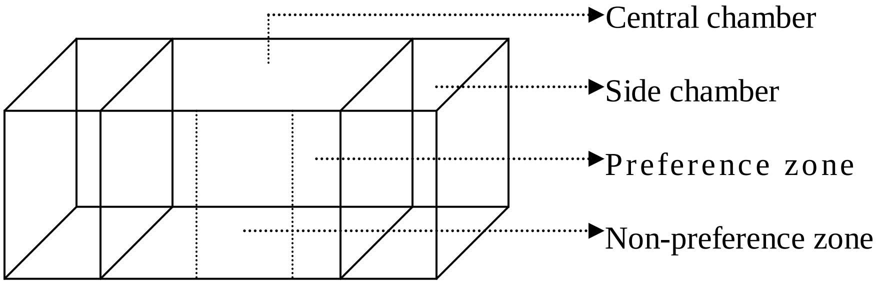


Figure 1. Diagrammatic representation of the apparatus used for testing the influence of familiarity on shoaling decision of climbing perch.

General protocol

Two stimulus shoals were introduced into each side chamber of the apparatus. After placing the presentation cage at the centre of the middle chamber, the test fish was introduced into it. Ten minutes were given to the fish to assess the stimulus shoals present in the side chambers. In order to avoid interference due to the presence of the experimenter, the presentation cage was suspended using a string tied to a pulley and the test fish was released into the arena by lifting the cage. The time spent by the test fish near either of the stimulus shoals (within 10 cm from the side chamber; preference zone) or in the central area (non - preference zone) of the middle chamber was recorded using a stopwatch, by sitting behind a black screen. The time spent by the test fish in the preference zone is taken as the indication of its preference for the shoal present in the adjacent chamber. The duration of each test was six minutes, after which the fish was removed from the testing arena and put back into their home tank. No test fish was used more than once with any stimulus shoal pair and new fishes were used in each trial of the three experiments. After the experiments, the fishes were released into their native ponds.

Three types of choice experiments were conducted and the basic protocol was same in all experiments.

Experiment 1: Influence of familiarity on shoal preference

To test the influence of familiarity on shoal preference, two stimulus shoals, one familiar and the other unfamiliar, of equal number (1:1 ratio) were presented in the side chambers. The familiar shoal was composed of ten fishes from the home tank of the test fish and the unfamiliar shoal comprised ten fishes taken from a different tank. Fishes for the stimulus shoals were selected randomly from the holding tanks with replacement so as to get a different combination of fish in each trial. 42 individual fishes were tested from seven different groups.

RESULT

The test fish spent only a short segment of total test period (< 0.5% of total time) in the non-preference zone, indicating the shoaling nature of climbing perch. When presented with a combination of familiar and unfamiliar shoals of equal size, the test fish prefered to stay near shoals consisting of familiar individuals (Fig. 2; Wilcoxon matched pairs signed rank test, $T = 27$, $N=7$; $P < 0.01$; Statistical programme KyPlot). The result demonstrates that climbing perch has a tendency to join familiar conspecifics.

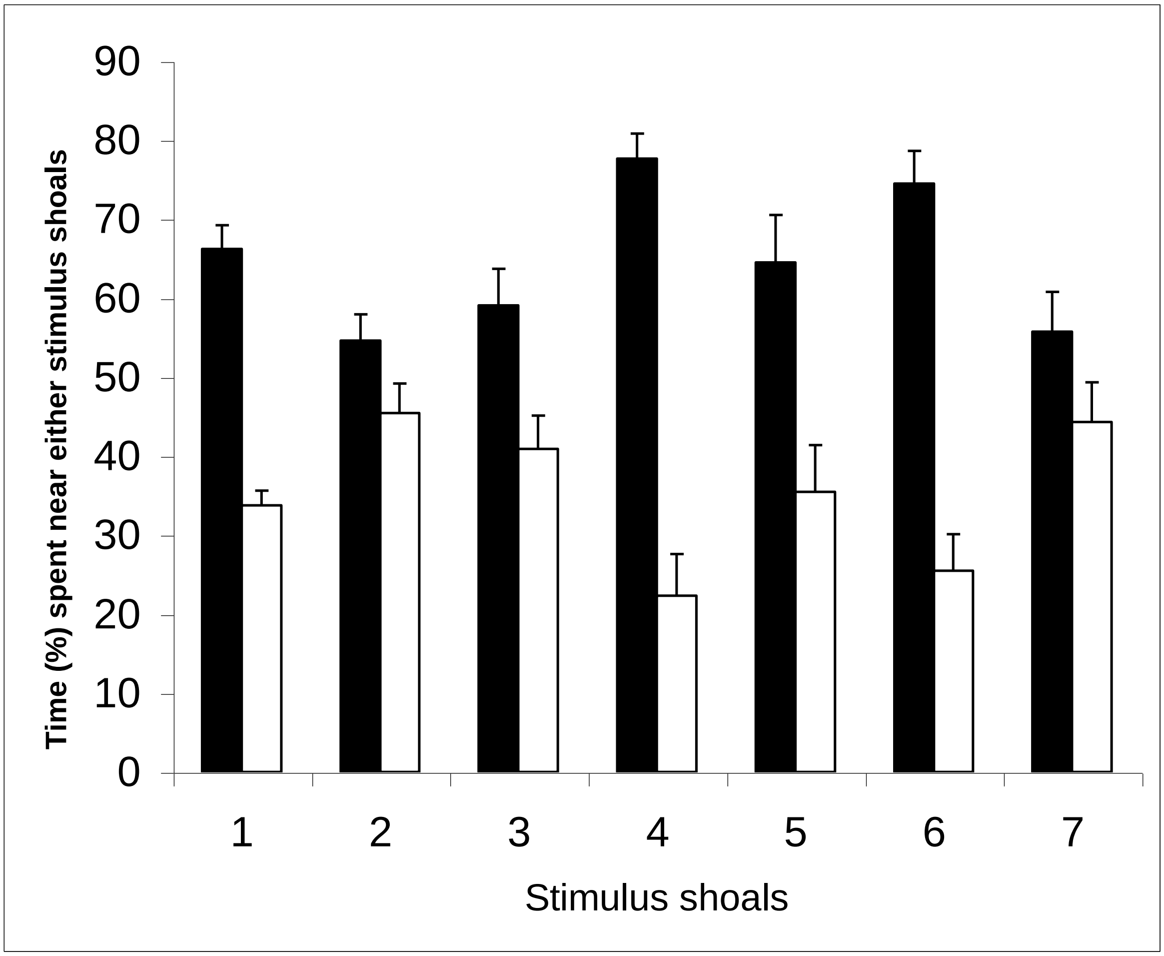


Figure 2. Preference of individual climbing perch for familiar / unfamiliar shoals
■ The mean % of time +SD spent near familiar shoal; □ the mean % of time +SD spent near unfamiliar shoal. N/n = 6 / 42

Experiment 2: Effect of shoal size on shoaling decision

In this experiment, shoal size preference of climbing perch was tested. Here, the test fishes were presented with two unfamiliar stimulus shoals selected from two separate familiarization tanks, in the following numerical size combinations i.e., 10 vs.10, 9 vs.11, 7 vs.13, and 4 vs.16 (ratio: 1:1, 1:1.2, 1:1.9 and 1:4 respectively).The total number of individuals in stimulus tanks was kept constant (20) in all experiments. 20 individual fishes selected from groups other than that formed the stimulus shoals were used as focal fishes.

RESULT

The test fish preferred to remain with the larger group. In fact, preference of the fish for larger groups, as indicated by the time spent by the test fish in the preference zone, increased with increase in the shoal size (Fig. 3). The preference for any group was not significant when the shoal size was in the ratio of 1:1 and 1:1.2 (10 vs. 10 and 9 vs. 11; $T = 67$, $N = 20$; $P > 0.05$ and $T = 58$, $N = 20$; $P > 0.05$, respectively). However, when the shoal size was changed from 1:1 to 1:1.9, the fish exhibited significant preference to the larger shoal (7 versus 13; $T = 159$, $N = 20$; $P < 0.01$). A highly significant preference for the larger shoal was exhibited by the test fish when presented with two unfamiliar shoals with a size ratio of 1:4 (4 vs. 16; $T = 190$, $N = 20$; $P < 0.001$). This shows that the size of the shoal has a predominant effect on the shoaling decision of this species.

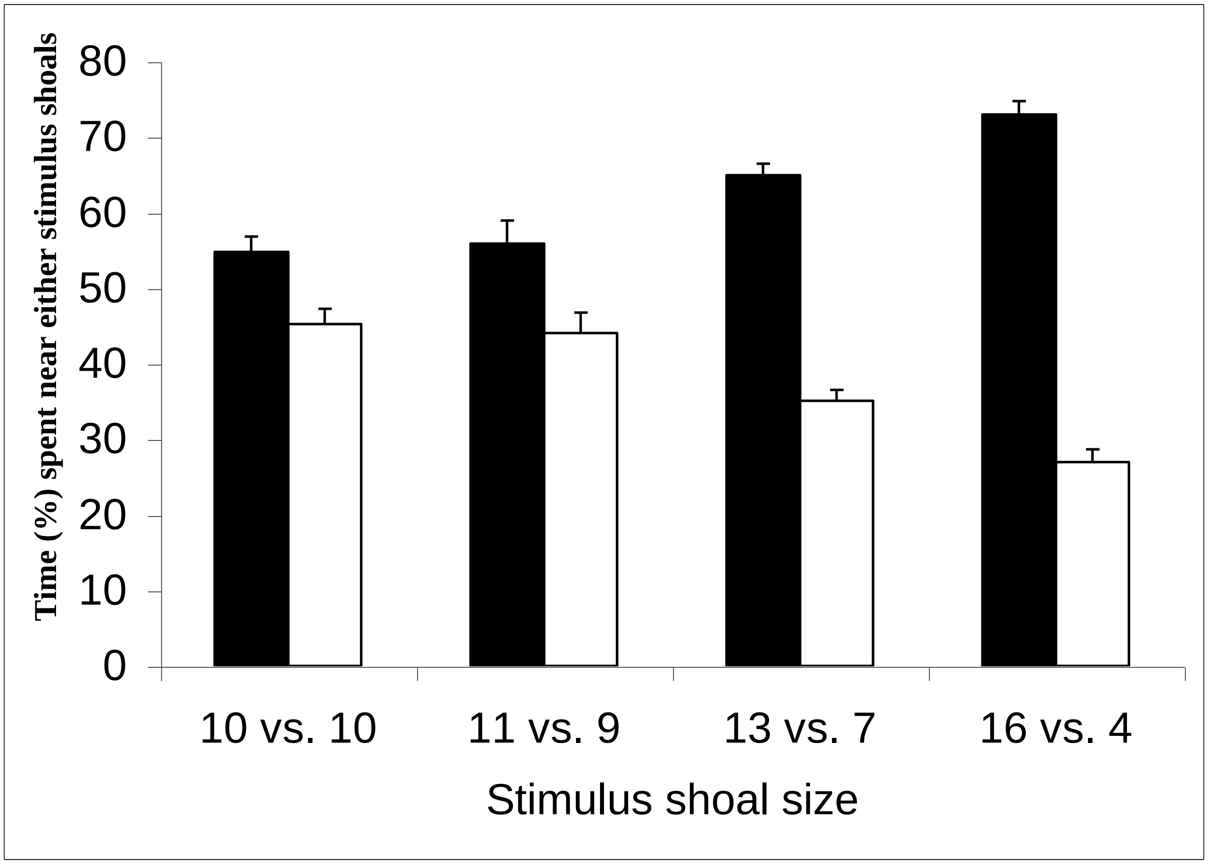


Figure 3. Preference of individual climbing perch for larger/smaller shoals

■ The mean % of time +SD spent near larger shoal. □ The mean % of time +SD spent near smaller shoal. N/n = 20 / 80

Experiment 3: Familiarity vs. shoal size

To determine the trade-off point of familiarity against shoal size, the test fish was given the same stimulus combination as in Experiment 2, except for the test for 1:1 ratio, for which the data was taken from the mean values of the outcome of all the 7 groups in Experiment 1. In contrast to the situation in Experiment 2, the smaller shoal was always composed of familiar fish and the larger shoal that of unfamiliar fish. 20 fish tested individually for each pair of shoals presented.

RESULT

It was observed that the climbing perch preferred a larger unfamiliar shoal to a smaller familiar shoal, when the effect of familiarity with shoal members over the preference for larger shoal was tested (Fig. 4). The preference for a larger unfamiliar shoal could be seen even at a shoal size ratio of 1:1.2 and 1: 1.9 (9 vs. 11; $T = 110$, $N = 20$; $P < 0.05$ and 7 vs. 13; $T = 110$, $N = 20$; $P < 0.05$). A highly significant preference for an unfamiliar larger shoal to a smaller familiar shoal was shown only when the ratio of the familiar shoal to unfamiliar shoal was 1: 4 (4 vs. 16; $T = 188$, $N = 20$; $P < 0.001$).

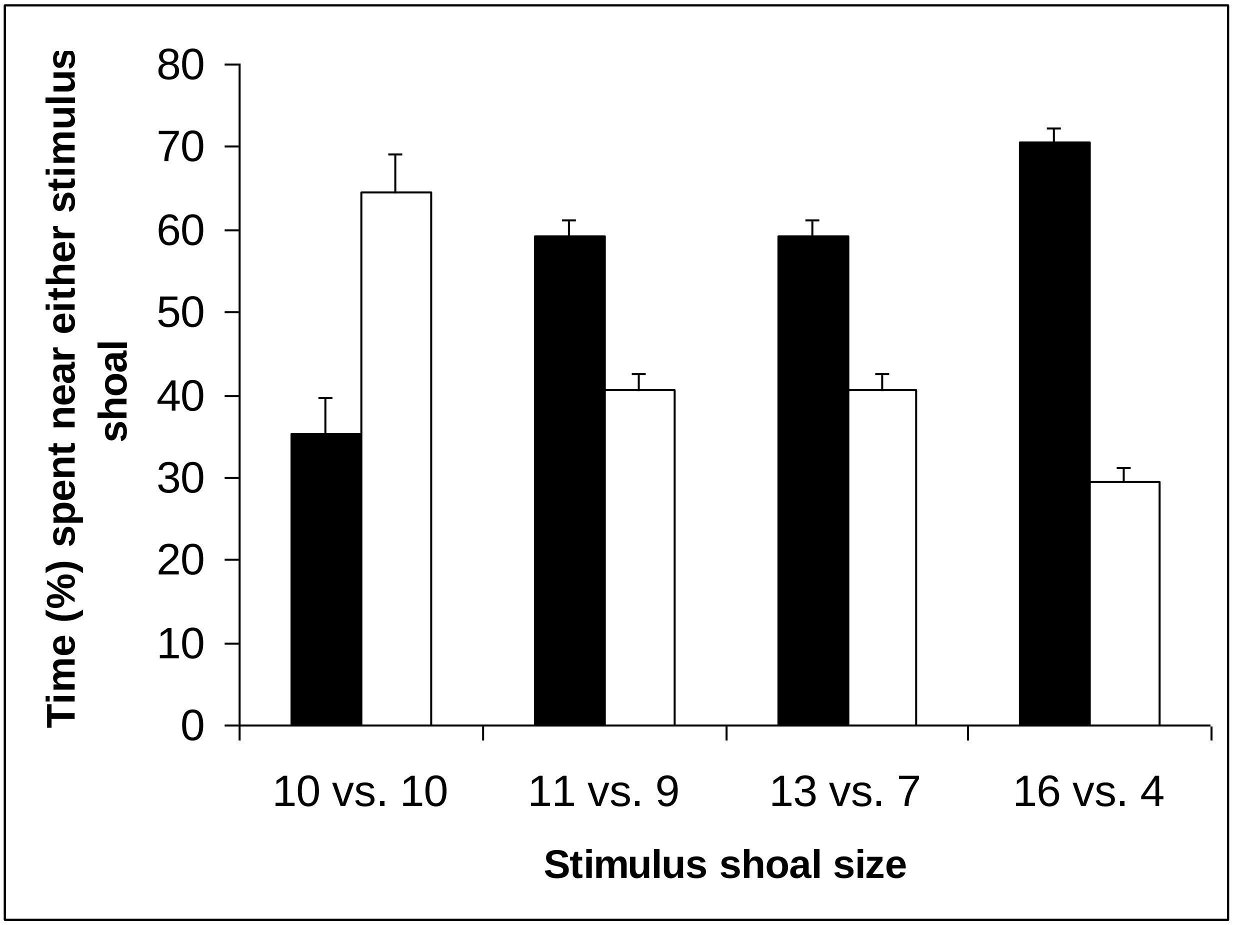


Figure 4. Preference of individual climbing perch for unfamiliar / familiar shoals
■ The mean % of time +SD spent near familiar shoal. ☐ The mean % of time +SD spent near unfamiliar shoal. N/n = 6 / 42

DISCUSSION

In the natural aquatic habitat, shoal formation and disruption are likely to occur due to several environmental and anthropogenic factors. It is reported, for example, that shoaling fishes have a natural tendency to move from one group to another when they happen to encounter with each other (Helfman, 1984; Svensson *et al.* 2000). In such situations, the majority of fishes have a tendency to join the larger group (Keenleyside, 1955; Ashley, *et al.* 1993; Lachlan, *et al.* 1998). Recently, Barber and Wright (2001) have effectively compared the strength of preference of an individual European minnows (*Phoxinus phoxinus*), for remaining with familiar shoal mates against other attributes of the group and found that familiarity can influence the shoaling decision.

Given a choice of familiar and unfamiliar shoals of equal size, climbing perch preferred to join the familiar group. Preference for the familiar shoal has been reported in several fish species belonging to different families. Examples: guppies (*Poecelia reticulata*; Lachlan *et al.* 1998) and rainbow fish (*Melanotaenia sp,* Brown, 2002). Chivers, *et al.*, (1995) describe this preference to join with familiar conspecifics is highly beneficial as it provides improved co-ordination of antipredator behaviours.

In a conflicting situation, where two shoals composed of unfamiliar individuals, but with variation in the number of shoal members were presented simultaneously, the climbing perch preferred to join the larger shoal and the preference always showed a positive correlation with shoal size. Similar affinity for larger shoals over smaller shoals has been reported in many species (Golden shiners *Notemigonus crysoleucas,* Reebs and

Saulnier, 1997; Guppies, Lachlan *et al.* 1998). This decision is highly beneficial to the fish as the life in larger group always provides more benefits than joining smaller groups (Pitcher and Parrish, 1993).

The present study indicates that, in climbing perch, acquaintance with conspecifics of a shoal can inhibit group desertion only to a limited extent. The lower limit value for desertion from a smaller familiar shoal to a larger unfamiliar shoal in climbing perch seems to be around the ratio of 1:1.2, which is lower than that shown by European minnows (Barber and Wright, 2001). They were shown to share their time equally between two shoals at a shoal size ratio of 1: 1.9 (7 familiar vs. 13 unfamiliar), (Barber and Wright, 2001). The tendency of climbing perch to prefer larger unfamiliar group to smaller familiar group of 1.2:1 points to a heightened dependence on group-size in its shoaling behaviour. It has been suggested that, in climbing perch familiarity benefits are perceived as equivalent at an approximate doubling of the size of the unfamiliar shoal, to that of familiar shoal (Binoy and Thomas, 2004).

It is reported that large size of prey groups considerably decreases the hunting success of various aquatic piscivorous predators (Mlinski, 1979; Tremblay and FitzGerald, 1979). It is therefore possible that the presence of voracious predators like *Channa punctatus* or *Channa marulius* in the natural habitat could have influenced the shoaling decision of climbing perch. Support for this hypothesis comes from the observation that a *Channa striatus* of length 16-20 cm (S.L.) was able to swallow a climbing perch of length 4-6 cm (personal observation). In such a situation, the decision to join a larger unfamiliar group that outweighs the benefits of remaining with a smaller familiar group is quite tenable.

Chapter II

Climbing perch recognizes and prefers members of familiar shoals to shoal with

INTRODUCTION

Though, once fishes were considered as organisms with three-second memory, recently it has been shown that they exhibit complex abilities like intraspecific and inter-specific communication skills, cooperation in the context of predator detection, capacity to transmit cultural traditions etc. (Laland *et al*. 2003; Griffith, 2003; Krause *et al.* 2000; Houde, 1997). In recent years, it has become evident that fish can discriminate one another through learning and experience (Dugatkin and Wilson, 1992; Dugatkin and Sih, 1995; Dugatkin, 1997; Krause *et al.* 2000). The ability to discriminate familiar from unfamiliar conspecifics (Brown and Smith, 1994) has been demonstrated in a wide variety of fishes like bluegill sunfish (Griffith, 2003), three-spined stickleback (Krause *et al.* 2000), fathead minnows (Houde, 1997) etc.

Fish can easily distinguish amongst conspecifics on the basis of obvious morphological differences. It has been shown that schoolmates of similar size are preferred by mackerel (*Scomber scombrus*), herring (*Clupea herengus,* Pitcher *et al.* 1985), minnows (*Phoxinus phoxinus*, Pitcher *et al.* 1986) and three-spined sticklebacks (*Gastrosteus aculeatus*, Ranta *et al.* 1992 a; b; Krause *et al.* 1996).

Recognition of individual conspecific is an expression of higher cognitive abilities of a species and is important in the contexts of decision-making (Krause *et al.*1996) like mate choice (Milinski *et al.* 1990), school/shoal selection (Brown and Colgan, 1986), and choosing an anti-predator strategy (VanHarve and Fitzgerald, 1988). Moreover, individual recognition is considered to be the basis of development of cooperation systems and thus the emergence of social system and altruism (Alfieri and Dugatkin, 2006).

Familiarity and recognition

Recent studies show that, there exist two different systems controlling the familiarity dependent recognition in fishes, i.e., condition dependant system and condition independent system (Griffiths, 2003). In both systems, experience with the conspecifics is the key factor leading to the development of familiarity.

Condition dependent system

In condition dependent system, fish learns and recognises the specific morphological characteristics of conspecifics, like colour, size etc. (Milinski *et al.* 1990). Condition dependent recognition allows the fish to discriminate among particular individuals over a very short time frame (only a few hours) to develop familiarity (Dugatkin and Alfieri, 1991). The ability to learn the identity of particular individuals and associate with them later during predator inspection by sticklebacks is an excellent example for the condition dependent familiarity and recognition (Milinski, *et al.* 1990).

Condition independent system

The condition independent familiarity and recognition is reported from a wide range of marine and freshwater fishes (Binoy and Thomas, 2004; Griffiths, 2003; Allan and Pitcher and Parrish, 1993). Differing from the condition dependent system, in condition independent system the individuals are recognised on the basis of familiarity obtained during the previous experience alone. Here, the time spent with the other individual is the core factor that determines the development of familiarity (Johnsson, 1997). In condition dependent familiarity, the experience and memory of the morphological cues are not as important as in the case of condition dependent system (Griffiths, 2003). The condition independent familiarity has been highlighted in the study of Chivers *et al.* (1995), where it is reported that familiar fathead minnows exhibit increased level of cooperation during the avoidance of predator attack. The preference for the association with poor competitors (Metcalfe and Thomson, 1995) is another context where fishes utilise condition independent familiarity.

Selection of the most cooperative conspecific during predator inspection

There are strong evidences that fish can distinguish between conspecifics in the context of antipredator behaviour. During predator inspection (where two or more fish approach a potential predator to assess its motivational status and likely threat), fish preferentially approach the predator in partnership with the most cooperative individual (Miliski *et al.* 1990a;b). These authors found that in sticklebacks the selection of the partner while assessing the motivational status of predator is not a random event. Instead, after getting familiarised with the extent of co-operative behaviour of each shoal mate, the fish actively chooses the most cooperative individual as partner. The time required to acquire the familiarity is only four inspection trials with that partner (Milinski *et. al.* 1990b). Predator inspection in partnership with the most cooperative individual is also reported in guppies (Dugatkin and Alfieri, 1991). These results indicate that fishes are able, not only to distinguish familiar individuals from unfamiliar conspecifics but also, to understand and predict the behaviour of the most cooperative familiar conspecific and respond differently towards different individuals.

According to Binoy and Thomas (2004) climbing perch is able to discriminate a familiar shoal from an unfamiliar one, where shoal size plays a decisive role in the shoaling decision. But there are reports supporting the view that the presence of familiar individuals in a shoal can influence shoaling decisions in many fishes (Griffiths, 2003). This chapter evaluates the question whether the climbing perch is able to identify and respond differentially towards isolated individual from a familiar and unfamiliar shoal.

MATERIALS AND METHOD

Familiarization

Climbing perches were familiarized with conspecific in aquaria of size 56 x 28 x 28 cm. Side walls of all familiarization aquaria were covered using black paper to cut off of any external interference. Steel grids placed on the top of the aquaria, prevented fishes from jumping out of water. Water level was maintained at a height of 25 cm.Ten fishes were allocated to each of the fifteen familarisation tanks and these fishes were kept as such for thirty days for familiarization. The fishes were fed with artificial food pellets (Higashimaru, Japan) *ad lib.* twice daily (morning and evening). Excess pellets were siphoned out thirty minutes after each feeding session. Water was changed with in an interval of ten days.

A conspecific from the home cage of the focal fish was introduced into one of the side chambers of the apparatus (described in Chapter 1). In the opposite side chamber, an unfamiliar conspecific fish (from a different tank) was introduced. The preference was recorded as mentioned in the general protocol (Chapter 1). 35 individual fishes were tested with different stimulus fish in each trial.

RESULT

The result shows that climbing perch introduced into the central chamber (experimental fish) spent only a few seconds (<0.5% of total time) in the non-preference zone and it preferred to spend more time near the familiar individual, compared to the unfamiliar individual (Wilcoxon matched pairs signed rank test, T = 485, N = 35; P<0.001, Fig.1). This result validate the hypothesis that climbing perch possesses the ability to recognize a familiar shoal mate even in isolation and prefers to join with the familiar conspecific than with an unfamiliar conspecific.

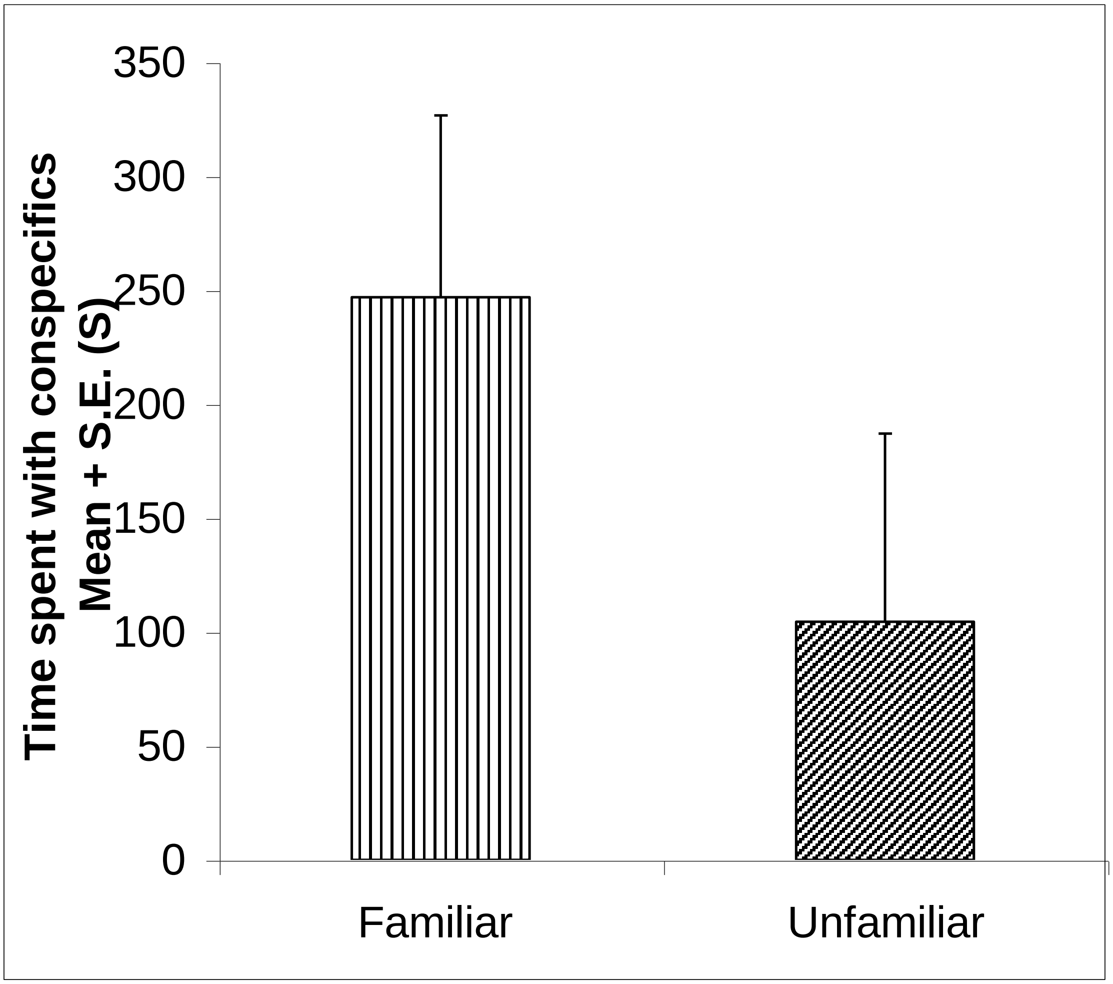


Figure 1. Preference of climbing perch for familiar/unfamiliar shoal mates; N=35.

DISCUSSION

The shoaling decision and shoal cohesiveness are heavily dependent on the ability of the fishes to recognize individuals (Brown and Smith, 1994). Recognition of shoal mates also helps to perform group manoeuvres more fruitfully, thus enhancing the benefit of shoal living (Pitcher and Parrish, 1993). Earlier study shows that the climbing perch prefers to spend more time with the shoal composed of familiar individuals, rather than with shoal formed of unfamiliar conspecifics (Binoy and Thomas, 2004). However, the size of the shoal has an overriding influence on the preference in shoal selection based on familiarity (Binoy and Thomas, 2004).

As a shoal living species, the ability for individual recognition in climbing perch reduces aggression among the shoal mates. For instance, during the initial days of stocking, climbing perches exhibited aggressive behaviour by nipping each other. But by day three, the aggressive displays reduced significantly and disappeared afterwards. It is possible that the observed reduction in aggression among group-housed climbing perch is a result of familiarity developed among the members as a result of living together.

One of the advantages of shoal living is said to be the efficiency of spreading information on food source rapidly among the members of the shoal (Chivers *et al.* 1995). Individual recognition and familiarity may further augment this effect. Certain fishes routinely change shoals and join other shoals composed of poor competitors (Metcalfe and Thomson, 1995). Assessment of the activities of shoal mates is crucial in the context of making decisions like, whether to stay in the same shoal or to join another during encounter with other shoals. Being a shoaling species, remembering and recognizing individual conspecifics of a shoal enables the climbing perch to take beneficial decisions and to enhance the advantages of group living.

Chapter III

The Influence of visual and olfactory cues on shoaling decision

INTRODUCTION

The primary form of social interaction in a shoal is the association and attraction towards conspecifics or aggression and repulsion of the intruders (Griffith, 2003). Prolonged interaction of an individual fish with conspecifics results in the development of familiarity, thus providing vital information on individual differences in the behaviour of shoal mates. This knowledge allows the fish to co-ordinate its behaviour with that of the group or to exploit the action of others for personal advantage (Chivers *et al.* 1995; Metcalfe and Thomson, 1995). Consequently, learning, remembering and recognizing the characteristics of conspecifics may be advantageous for shoaling fishes in attaining a stress free life (Griffith, 2003). Hence, familiarity can be considered as one of the key factors that contribute to shoal cohesion in fish.

Even though, many species of fishes possess the ability to recognize a shoal composed of familiar individuals (Ward and Hart, 2003; Binoy and Thomas, 2004; 2006), the cues by which information about other individuals or a shoal are gathered may vary from species to species (Ward *et al.* 2007). In fishes, the cues involved in the development of familiarity are contentious. Many species prefer olfactory cues (emitted by the conspecifics or heterospecifics), while others depend on visual cues (Griffiths, 2003).

Many studies show that the chemicals transmitted through urine acts as the signal for olfactory recognition of familiar members (Moore *et al.* 1994). Juvenile salmonids and juvenile Arctic charr have been shown to transmit and assess signals derived from chemicals in urine for the recognition of individuals (Olsen, 1987; Moore *et al.* 1994). A study conducted by Olsen *et al.* (2002) also reveals that this signal is composed of a range of different chemicals whose production is controlled by many factors like diet, social status etc.

Recent studies suggest that fishes consuming similar diet can develop familiarity and preference among each other based on the odour of food materials (Morrel *et al.* 2007). Ward *et al.* (2005) demonstrated that sticklebacks exhibit familiarity dependent behaviours to unfamiliar conspecifics collected from a habitat with similar physico-chemical conditions. This finding demonstrates that chemistry of water plays a significant role in the establishment of familiarity with shoal mates.

Several other species utilize visual cues for recognizing identity of frequently encountered individuals over time (Griffith, 2003). For example, angelfish (*Pterophyllum scalare*, Gomez-Lapaza and Fuente, 2007) and zebra fish (*Danio rerio*, Engezger *et al.* 2004) recognize familiar shoal mates using visual characteristics. Electric fishes depend on weak electric pulses emitted by conspecifics as a cue for the identification of familiar individuals or group (Kramer, 1990). Some other studies show that many fishes require a combination ofvisual and olfactory cues for recognition of familiars (Arnold, 2000). For example, in rainbow fish individual recognition is severely affected when the visual cues were separated from the olfactory cues. The influence of visual or /and olfactory characteristics of conspecifics on the shoaling decision of climbing perch is examined in this chapter.

MATERIALS AND METHODS

Familiarization

Healthy fishes of similar size (standard length 6 ± 1 (SE) cm) were selected. Familiarization with stimulus fish was conducted in aquaria of size 56 x 28 x 28 cm. Side walls of all familiarization aquaria were covered using black paper to cut off any external interference. Steel grids placed on the top of the aquaria prevented fishes from jumping out of water. Water level was maintained at a height of 25 cm. The fishes were fed with artificial food pellets (Higashimaru, Japan) *ad lib.* twice daily (morning and evening). Excess pellets were siphoned out thirty minutes after each feeding session. Water was changed with in an interval of ten days.

Apparatus

All experiments were conducted in a 70-l aquarium (85 x 32 x 32 cm) divided into three compartments, two side chambers (16 x 32 x 32 cm each) and a central chamber (53 x 32 x 32 cm), using opaque acrylic sheets with perforations (pore size: 0.25 cm diameter and distribution: two pores / cm^2), (Binoy and Thomas, 2006). Three sides of the aquarium were covered using black paper. The focal fish was introduced individually into the central compartment in a presentation cage made of transparent perforated acrylic sheets (15 x 10 x 27 cm) with a sliding door on the top (as mentioned in the chapter 1). The bottom of the presentation cage was open so that the focal fish can be released in to the experimental arena by raising the cage. The water level in the apparatus was kept at 28 cm. A compact fluorescent lamp (20 w) lighted the whole set-up from above.

Experiment 1: Influence of olfactory cues

Each of the ten familiarization aquaria was divided into two equal compartments using opaque perforated acrylic sheet (pore size: 0.25cm diameter and distribution- two pores / cm^2). Five fishes were allocated to each compartment of all the ten aquaria (G1). This set up allowed the fish residing in one chamber to have access with the olfactory cues emanating from conspecifics housed in the adjacent chamber, without having any visual contact (Fig. 1a).

After thirty days of familiarization with olfactory characteristics of the conspecifics, these fishes (G1) were tested for their shoaling preference. Five fishes from the side chamber of the home tank of focal fish [whose odour was familiar to the focal fish (G1)], were introduced into one of the side chambers of the testing apparatus. In the opposite side chamber five unfamiliar fishes (kept in a different familiarization tank) were housed (Fig. 2a). This arrangement was kept undisturbed for half an hour so that the odour-producing chemicals (if present) spread from both side chambers and diffuse into the central chamber forming horizontal strata of concentration gradients (Mc Lennan and Ryan, 1999; Neff and Sherman, 2005). The distribution and circulation of olfactory cues were confirmed by visualization using Methylene blue as described in dye tracer test (Neff and Sherman, 2005). The focal fish was then placed in the presentation cage and its shoaling decision was recorded using the general procedure discussed in the Chapter 1. The duration of each test was six minutes, after which the focal fish was placed back into its home tank. The apparatus was drained and cleaned thoroughly after each trail. 31 individual fishes were tested in this experiment.

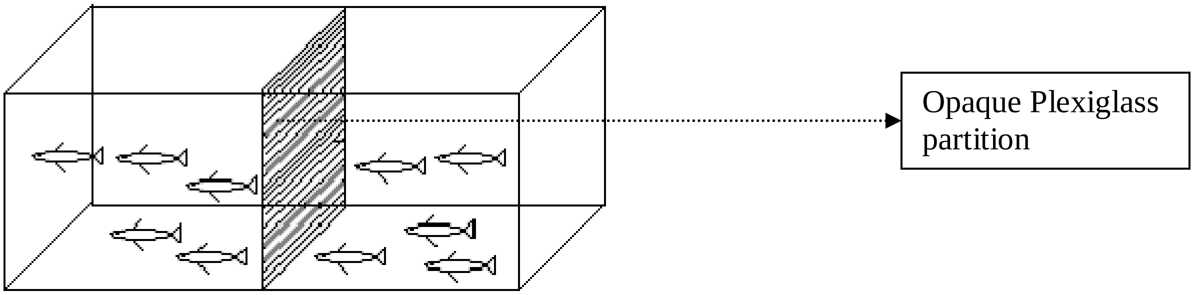


Figure 1 a. Diagrammatic representation of the setup used for the familiarization of climbing perch with olfactory stimuli produced by the conspecifics (Exp. 1).

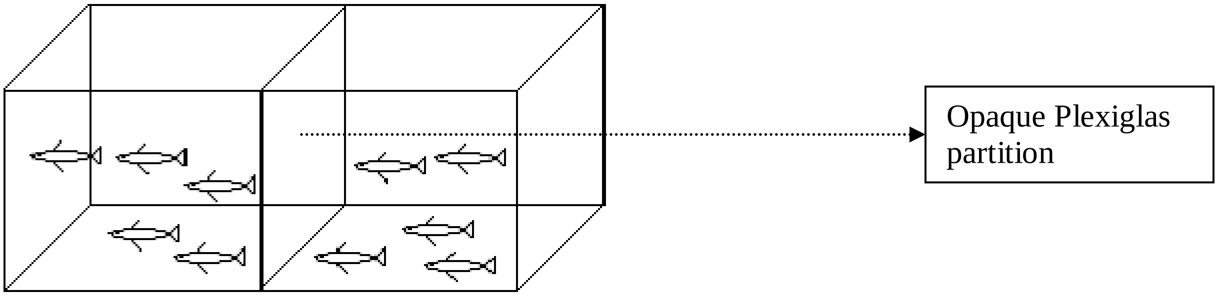


Figure 1 b. Diagrammatic representation of the setup used for the familiarization of climbing perch with the visual characteristics of the conspecifics (Exp. 2).

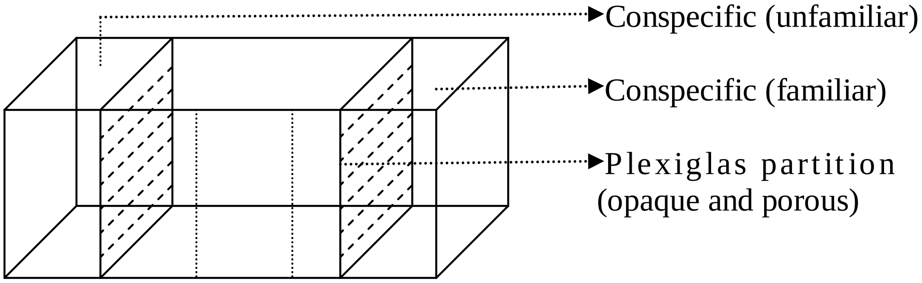


Figure 2a. Apparatus used for testing the influence of olfactory cues of conspecifics on the development familiarity in climbing perch.

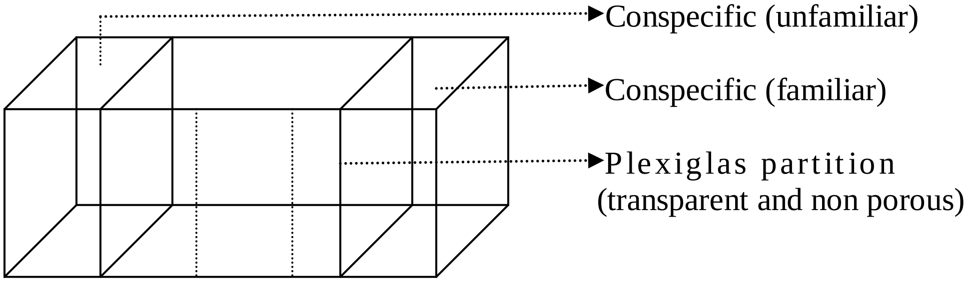


Figure 2 b. Apparatus used for testing the influence of visual traits of conspecifics on the development familiarity in climbing perch.

Experiment 2: Influence of visual cues

The influence of visual cues on the recognition of familiar shoal was tested using climbing perch familiarized with only the visual characteristics of conspecifics. Here, five climbing perch were housed in each chambers of a familiarization aquarium (56 x 28 x 28 cm) partitioned in to two equal sized compartments using transparent Plexiglas sheets (G2). This arrangement isolated the fish kept in one chamber from all other stimuli, except visual cues originating from conspecifics housed in the adjacent chamber (Fig. 1b). Ten replica of this arrangement was created and the fishes were kept as such for thirty days for the development of familiarity.

The shoaling preference of the focal fish from G2 was tested in a 70-l aquarium (85 x 32 x 32 cm; Fig. 2 b) divided into three compartments, two side chambers (16 x 32 x 32 cm each) and a central chamber (53 x 32 x 32 cm) using transparent Plexiglas sheets. Five individuals housed with the focal fish in the side chamber of the familiarization tank were allocated as the stimulus shoal in one side chamber, and in the opposite side chamber, five individuals from an unfamiliar shoal (from a different tank) were introduced. Ten minutes were given for the focal fish to assess conspecifics present on either side of the arena. The shoaling preference was tested using 31 individual fish as described in experiment 1.

Experiment 3: All cues vs. visual cues

The efficacy of visual cues were compared with effectiveness of the combination all cues emitted by the conspecifics during development of familiarity was tested in this experiment. Here, ten fishes were lodged together (G3) in each of the five familiarization aquarium (56 x 28 x 28 cm) without any partition, so that they have access to all cues emitted by their conspecifics. In this experiment also the duration of familiarization was thirty days. These fishes (G3) were tested for their preference using the procedure described in Experiments 2. One stimulus shoal was composed of five fishes from the home tank of the focal fish and the other comprised of five fishes from an unfamiliar shoal. Transparent Plexiglas sheets with perforations were used as the partition wall of the apparatus, which allowed the focal fish to access both visual and olfactory characteristics of the stimulus fish kept in the side chambers of the apparatus. The time spent by the focal fish of experiment 2 and experiment 3 near the familiar shoal were compared using Student's t test.

RESULTS

The dye tracer test revealed that the olfactory cues produced by the fishes kept in the side chambers of the apparatus will disperse to the middle chamber through the pores of partition wall, forming strata of concentration gradient. The result of experiment 1 shows that the test fish failed to exhibit any significant preference to either of the stimulus shoals, when one shoal was composed of familiar (with olfactory cue) conspecifics and the other with unfamiliar conspecifics (paired t test ; t_{30} =1.0512; P>0.05; Fig. 3). By contrast, when presented a combination of unfamiliar shoal and a shoal of individuals with familiar visual characteristics, the test fish always preferred to spend more time with the familiar shoal (paired t test ; t_{30} =-3.7968; P<0.001). In addition, there was no variation in the time spend by the focal fish of experiment 2 and experiment 3 near the familiar shoals (t test; $t_{30} = 1.10$, $P>0.05$; Fig. 4). This result shows that there is no variation in the acquisition of familiarity or the familiarity dependent preference, if visual cues are provided with a combination of all other stimuli emitted by the conspecifics.

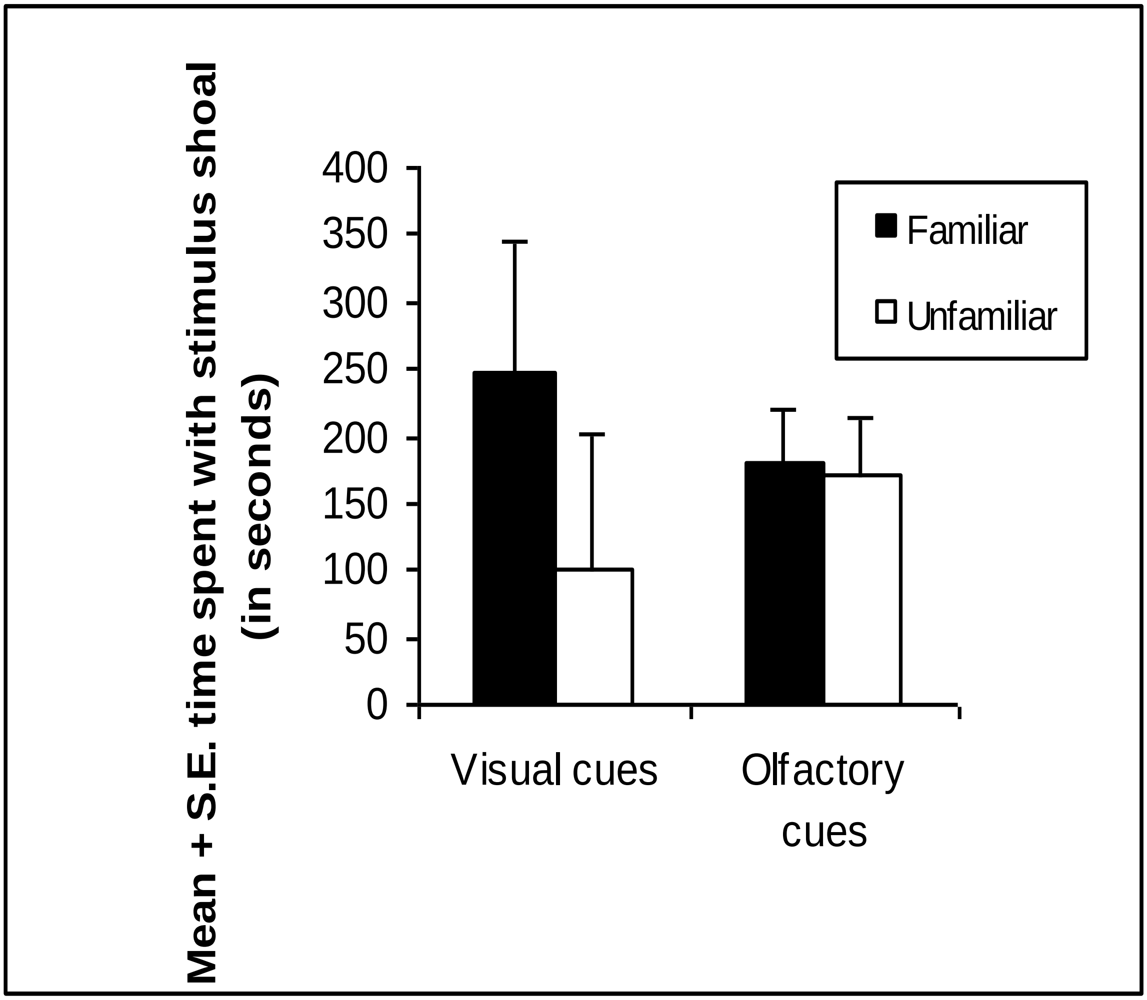


Figure 3. Preference of individual climbing perch for familiar (with visual cues or olfactory cues) / unfamiliar shoals. ***N* =31**

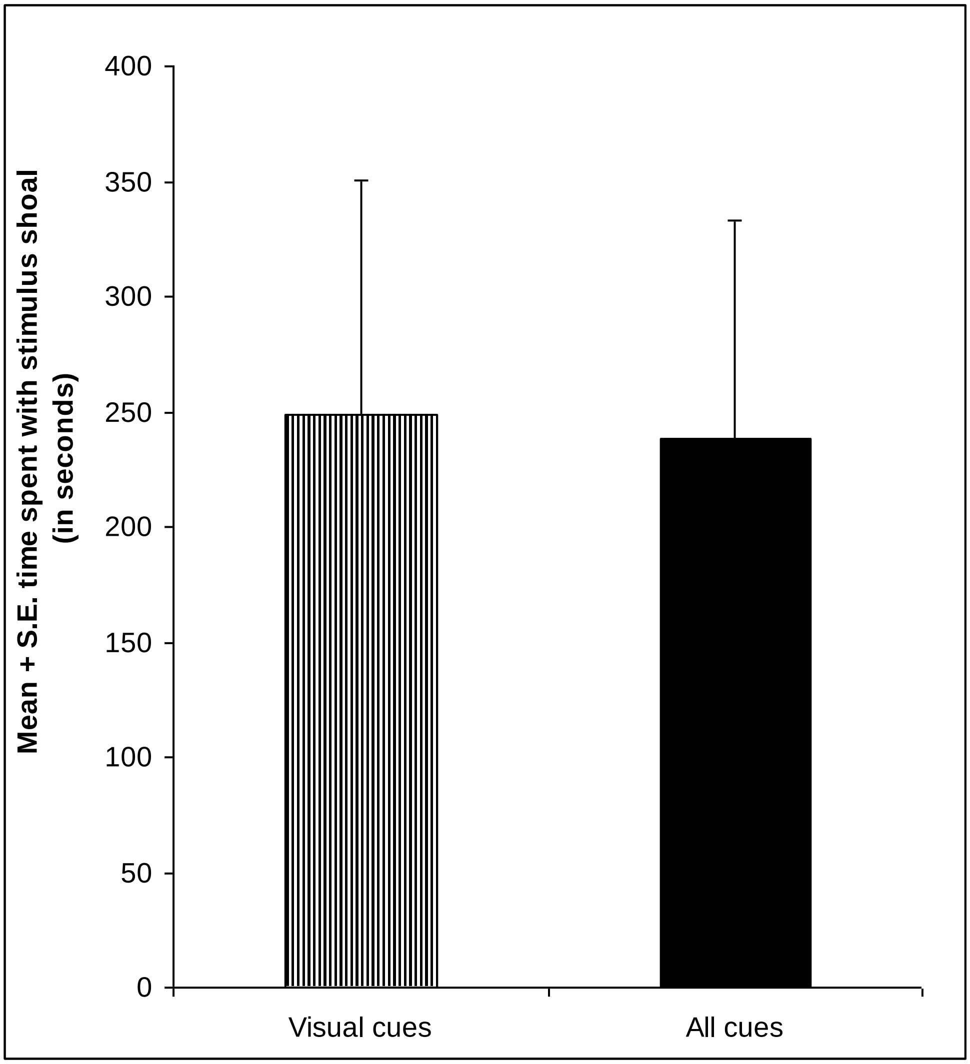


Figure 4. Preference of individual climbing perch for shoals with familiar visual cues/ all cues. ***N*** = 31

DISCUSSION

The cues involved in obtaining information about the identity of conspecifics and development of familiarity are being intensely analyzed using many species of marine and freshwater fish species (Griffiths, 2003; Ward and Hart, 2005; Ward *et al.* 2005). Most of the results show that fishes very often use olfactory cues than visual stimuli in the context of individual and shoal recognition (Ward *et al.* 2007). For example, Brown and Smith, (1994) have demonstrated that fathead minnows failed to recognize familiar shoal mates based on visual characteristics alone, at the same time they were able to express preference to olfactory cues of familiar conspecifics. Additionally, Ward *et al.* (2005) suggest that sticklebacks recognize familiar individuals by self referencing based on olfactory cues. Their study also reveals that this fish preferred to join unfamiliar shoals, if the members are with odour similar to the diet or habitat of the focal fish.

Surprisingly, climbing perch never showed any preference towards the shoals with familiar olfactory characteristics. However, they preferred and spend significantly more time near the shoal of individuals whose visual traits were familiar. Utilization of visual traits of conspecifics in assessing and making a decision to join a shoal has been reported in several fish species (Hoar and Krause, 2003). For example, in zebra fish it is possible to develop individuals with varying types of pigment pattern. This fish always preferred to join a shoal of individuals with familiar pigment pattern, a visual cue (Engezer *et al*. 2004). According to Hoare and Krause (2003), the size of shoal mate, another visual parameter, can influence the shoaling decision of a fish. Many species prefer to join shoals composed of individuals with similar size and free ranging fishes may frequently shoal with heterospecifics, if they are well matched in size (Krause *et al.*

1996). The size assorted shoaling is reported in sticklebacks (Peuhkuri *et al.* 1997), minnows (Ward and Krause, 2001), capelins and sardines (Fréon and Mislund, 1999). Additionally, Pritchard *et al.* (2001) demonstrated that zebra fish assesses the activity level of the conspecifics and joins a shoal of active conspecifics, another illustration for the utilization of visual cues while reaching a shoaling decision.

Anatomy of the climbing perch brain also supports the view that visual sense plays a dominant role over olfactory system in this fish. In this species, instead of olfactory bulbs there is only a pair of well developed olfactory lobe with short olfactory tract (Mookerjee and Mazumdar, 1946; Bersa, 1997). Considering all these features Bersa (1997) suspects that climbing perch is totally dependent on visual system for gathering information about its environment. Further studies will elucidate a clear picture of the mechanism behind the development of familiarity in climbing perch.

Chapter IV

Cross species familiarity and shoaling decisions

INTRODUCTION

In nature, mixed species group living is exhibited by a number of species from a wide range of taxa (Sinclair, 1985; Fitzgibbon, 1990; Metcalfe, 1989). Fishes are not an exception to this and mixed species shoaling is observed in many species (Allan and Pitcher, 1986; Ward *et al.* 2002a; Ward *et al.* 2004). Multi-species fish groups have been reported from varied aquatic escosystems including shallow freshwater bodies (Krause *et al.* 1996; Peuhkuri *et al.* 1997), tropical and sub tropical reefs (Sweatman, 1983; Dafni and Diamant, 1984; Overholtzer and Motta, 2000) and temperate pelagic regions (Hobson, 1963; Fréon and Mislund, 1999). Hoare *et al.* (2000) have pointed out that the majority of shoals in the littoral zone of a Canadian freshwater lake are composed of more than one species.

As in the case of monospecific shoaling, association with heterospecifics is also beneficial. Mixed species group living reduces the cost of vigilance if the member species face threat from a common predator (Metcalfe, 1989). In the context of predator attack, being in a large group provides more benefits of dilution effect than assorting into smaller monospecific groups (Fitzgibbon, 1990; Pitcher and Parrish, 1993). Mixed species group living provides additional benefits, if the member species exploit different resource niches (Sasvari, 1992). Additionally, juveniles of different species are found to form aggregations as they are more vulnerable to predators during early stages of development (Lightfoot and Jones, 1996).

Phenotypic oddity, which makes the odd member in a group more conspicuous and vulnerable to predation, is one of the major costs of heterospecific shoaling. Consequently, closely related species are more likely to form mixed species shoals, as this strategy considerably reduces the disadvantages of phenotypic oddity (Overholtzer and Motta, 2000). It could be suggested that a multispecific fish shoals may result when the antipredator benefits gained from the membership of a large shoal outweigh the costs of phenotypic oddity (Hoare and Krause, 2003; Landeau and Terborgh, 1986) and resource partitioning between different species reduces the competition for food and other basic needs (Ehrlich and Ehrlich, 1973).

Enhanced benefits of shoaling with familiar individuals can be achieved not only by shoaling with conspecifics, but also with heterospecifics (Ward *et al.* 2003). Hence, familiarity with members of heterospecific shoal considerably influences the shoaling decision of a fish. For example, chub *(Leuciscus cephalus*), a fish with natural tendency for shoaling with conspecifics, reallocates its preference when the heterospecific shoal is composed of familiar individuals of European minnows (Ward *et al.* 2003).

Different species of fishes make use of diverse strategies for the acquisition of heterospecific familiarity. According to Warburton and Lees (1996), ‘imprinting’ the characteristics of the fishes encountered and familiarized during the early phase of life functions as the basis for recognition of heterospecifics. These authors have demonstrated that guppies reared with heterospecific sword-tails exhibit familiarity based preference for heterospecifics over conspecifics. On the other hand, Ward *et al.* (2005; 2007) suggest that familiarity with the habitat cues, like water chemistry and the composition of food materials consumed, influence the decision to join a heterospecific shoal. Their study shows that threespined sticklebacks developed preference for heterospecific nine-spined sticklebacks (*Pungitius pungitius*) collected from similar habitats and living on similar diet. Hence, Bryant and Atema, (1987) suggest self referencing as the mechanism behind the acquisition of odour dependent familiarity in fish.

Acquisition of familiarity with an unfamiliar fish (conspecific or heterospecific) is a time dependent process. According to Griffiths and Magurran (1997a;b) guppies require twelve to fourteen days to develop familiarity based shoaling preference. However, a recent study by Ward *et al.* (2005) revealed that three-spined sticklebacks need twenty four hours to establish familiarity with heterospecific nine-spined sticklebacks. Further more, this study also states that full fledged expression of heterospecific familiarity is correlated with the duration of experience and may take ten to fourteen days.

Four different aspects of heterospecific shoaling are examined in this chapter:

1) What shoaling decision will a climbing perch take when two shoals of equal size, one composed of unfamiliar conspecifics and the other composed of unfamiliar heterospecifics, are presented simultaneously?

2) Whether climbing perch possesses the ability to develop familiarity with shoals of heterospecifics?

3) How long-term experience with heterospecifics influences the shoaling decisions of this species?

4) Earlier results (discussed in the chapter III) reveal that climbing perch relies more on the visual characteristics of their conspecifics to acquire familiarity with shoals of

conspecifics. Hence, the question whether morphology of heterospecifics has any effect on the development of familiarity and subsequent shoal preference in climbing perch was also analysed.

MATERIALS AND METHODS

Heterospecifics and holding conditions

The heterospecifics used in the present study were Malabar mystus (*Mystus occulatus*), a catfish, and tilapia (*Oreochromis mossambicus*), a cichlid fish. Malabar mystus were collected from channels in paddy fields of Irinjalakuda and tilapia were collected from aquaculture ponds. No attempt was made to sex the fish, as the natural population of these fishes occurs in heterosexual groups (personal observation). Fish measuring 6 ± 2 cm (S.L. ± SE) were selected. In order to avoid potential confounding effect of assortment by body length (Ward and Krause, 2001), heterospecifics and climbing perch of similar body length were used in all experiments.

All fishes were fed with artificial food pellets (Higashimaru, Japan) *ad lib.* twice daily (morning and evening). Excess pellets were siphoned out thirty minutes after each feeding session. Water was changed once in ten days. All experimental fish were found to be healthy at the end of the experiments and they were released back into their native habitats.

Familiarization

Climbing perch were familiarized with heterospecifics in aquaria (60 X 30 X 30 cm) covered with black paper on four sides to isolate the fish from all external cues. Steel grids placed on the top of the aquaria prevented the fishes from jumping out of water. Washed river sand spread evenly on the bottom served as the substratum in the familiarization aquarium. Water was filled up to the height of 25cm. 20 W white florescent lamp fixed 35cm above each aquarium illuminated tanks. 31 individual climbing perch were tested in each experiment.

Experiment 1: Unfamiliar conspecifics vs. unfamiliar heterospecifics

To investigate the shoaling decision of climbing perch, when presented with shoals of unfamiliar conspecifics and unfamiliar heterospecifics, 16 climbing perches were allocated into each of the eight familiarisation tank (size 60 x 30 x 30 cm; G1). These fishes were kept as such for 7 days to acclimatize with the laboratory condition and the shoaling decision was tested in the apparatus described earlier (Chaper 1).

In one of the side chambers of the apparatus, five unfamiliar tilapia and in the opposite side chamber five unfamiliar conspecifics were introduced (Fig. 1a). One fish from G1 was introduced in to the presentation cage. The time spent by the test fish near either of the stimulus shoals (within 5 cm from the side chambers - preference zone) or in the central area (non - preference zone) of the middle chamber after the release was recorded. The apparatus was drained and cleaned thoroughly after each trail.

The same protocol was carried out using other 31 individual climbing perch from other aquaria of G1 as focal fish. Here, the stimulus shoals were composed of five unfamiliar conspecifics and five unfamiliar Malabar mystus (Fig. 1 a).

Experiment 2: Unfamiliar conspecifics vs. familiar heterospecifics *(30 days of familiarization)*

A total of 16 fishes constituting of 8 climbing perch and 8 tilapia were allocated to each of the ten aquarium prepared for the purpose of heterospecific familiarization (G2). Ten replicates of another combination comprising 8 climbing perches and 8 Malabar mystus were also arranged. Each group was maintained for 30 days in the familiarization aquarium.

To test the influence of familiarity on shoaling decision of climbing perch, a shoal of five tilapia familiarized with the focal fish (from the home tank of focal fish) for a period of one month, was introduced in to one of the side chambers of the apparatus (Fig. 1b). Five unfamiliar conspecifics were placed in the opposite side chamber. The decision to join a shoal was tested following the basic testing procedure mentioned in experiment 1.

This experiment was repeated using individual climbing perches from other familiarization tanks of G2, by presenting five unfamiliar conspecifics and five familiar Malabar mystus (one month familiarity) as stimulus shoals.

Experiment 3: Unfamiliar conspecifics vs. familiar heterospecifics (90 days familiarization)

In this experiment, the influence of long term (90 days) experience with heterospecifics and its implication on the shoaling decision of climbing perch was tested. Here, 8 climbing perches were lodged with 8 Malabar mystus in a familiarization aquarium (G3). Another combination of 8 climbing perch and 8 tilapia were also kept for familiarization in another aquarium (G3). Six replicates of each combination were prepared. These fishes were kept as such for 90 days for the acquisition of familiarity. The shoaling preference of climbing perch (from G3) was analyzed by presenting a combination of shoals of unfamiliar conspecifics and familiar heterospecifics. Individual climbing perch from different familiarization tanks (G2) were tested with unfamiliar conspecifics- familiar heterospecifics (tilapia /Malabar mystus) combination (Fig. 1b) by following the procedure mentioned in experiment 2.

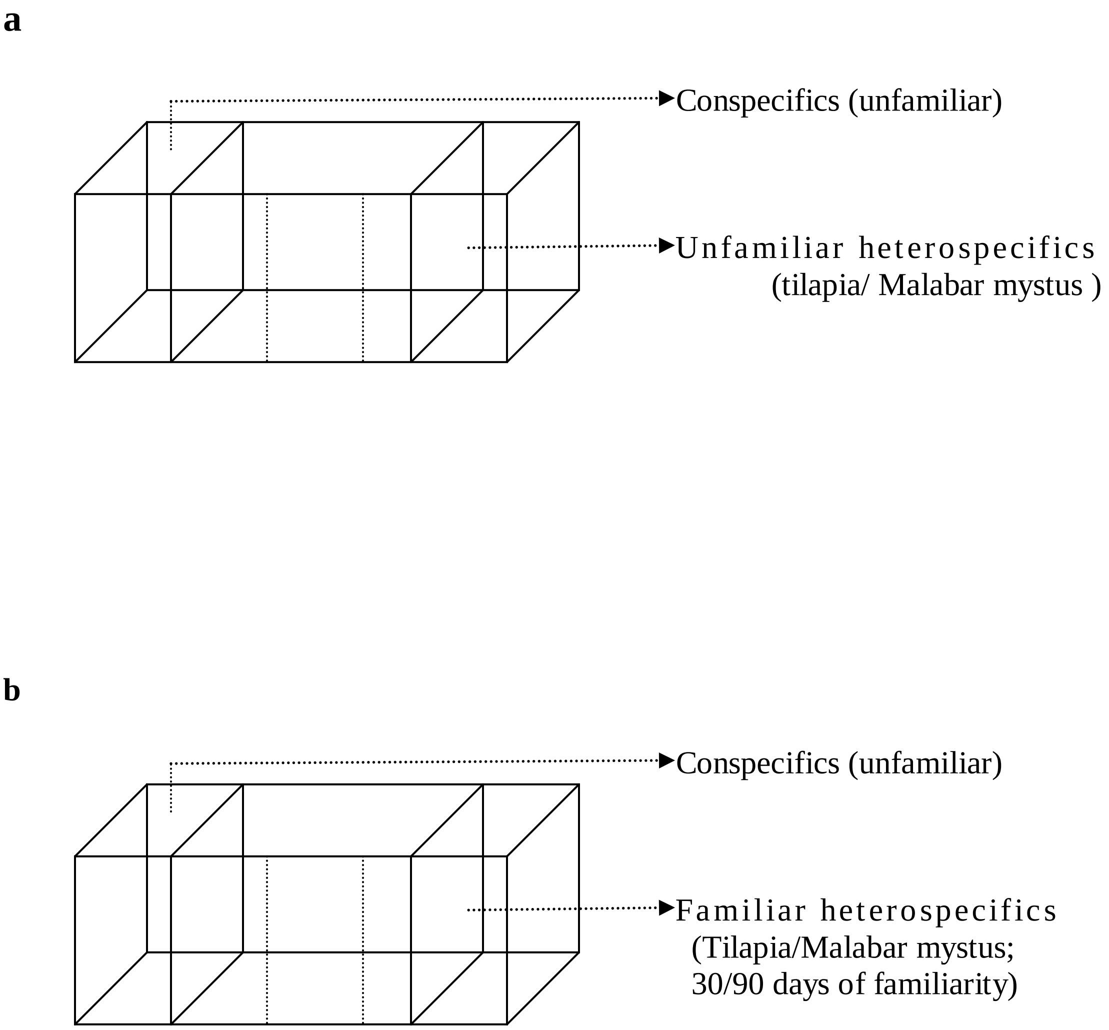


Figure 1. Diagrammatic representation of the experimental setup used for the analysis of development of familiarity with heterospecifics in climbing perch (a, b heterospecicfic: a cichlid fish, tilapia; c, d heterospecicfic: a catfish Malabar mystus)

RESULTS

Climbing perch preferred to join the shoal of unfamiliar conspecifics when presented simultaneously with stimulus shoals of unfamiliar conspecifics and unfamiliar heterospecifics (tilapia or Malabar mystus; Fig.1). Results of the experiment 2 show that keeping the climbing perch with heterospecific tilapia or Malabar mystus for 30 days, failed to develop any sort of association preference (Fig.2). However, climbing perch exhibited a clear cut preference to the shoal of familiar heterospecifics, tilapia, after living with with them for 90 days (ANOVA, $F_{2,\ 90} = 11.286$; $P < 0.\ 05$). By contrast, climbing perch was not able to develop familiarity dependent preference for the shoal of Malabar mystus, even after living together for 90 days (ANOVA, $F_{2,\ 90} = 1.9157$, $P>0.05$; Fig.3).

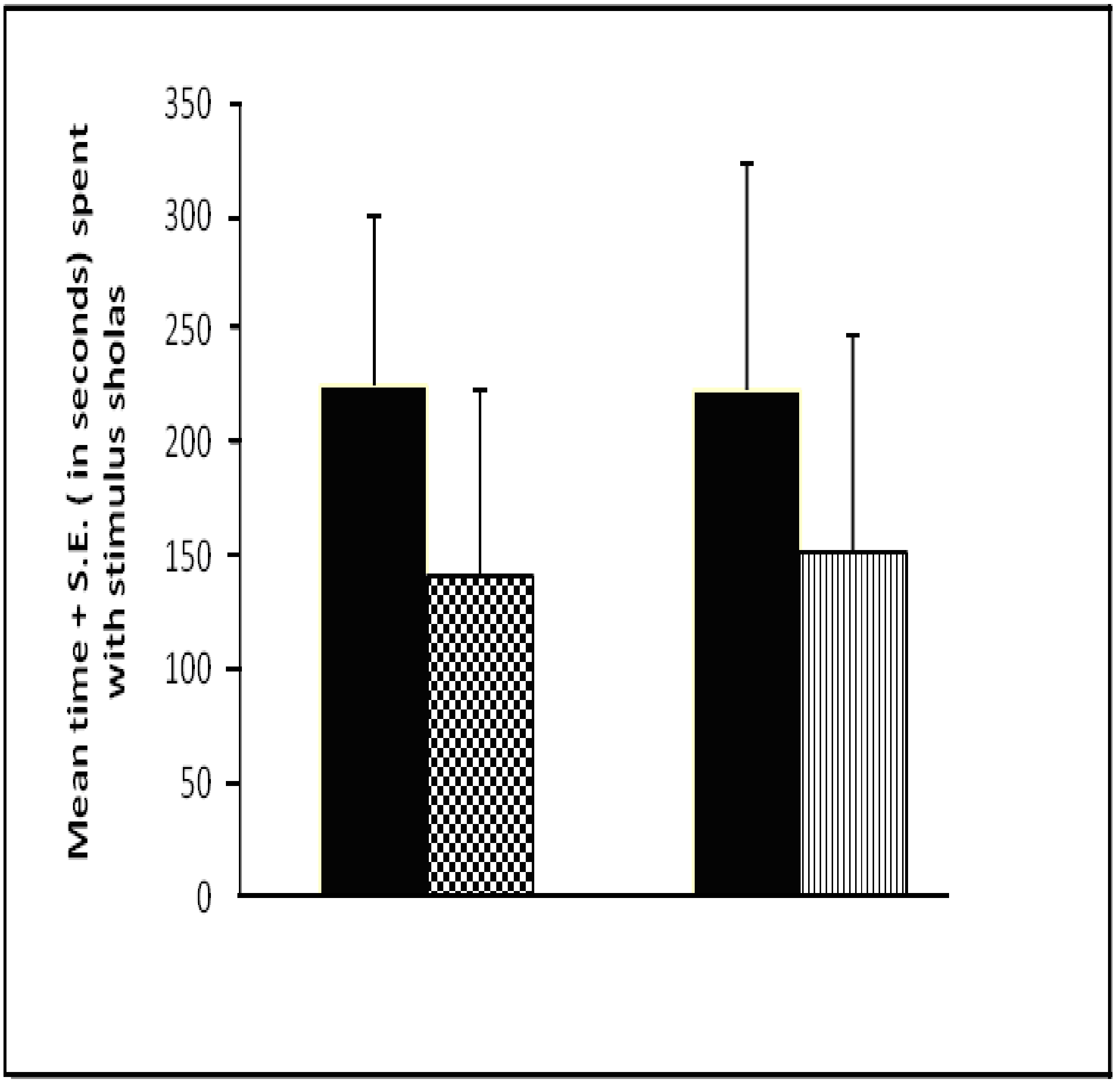


Figure 1. Preference of climbing perch for shoal of unfamiliar conspecifics ■ / unfamiliar heterospecifics (tilapia▦) and (Malabar mystus ▥);N=31.

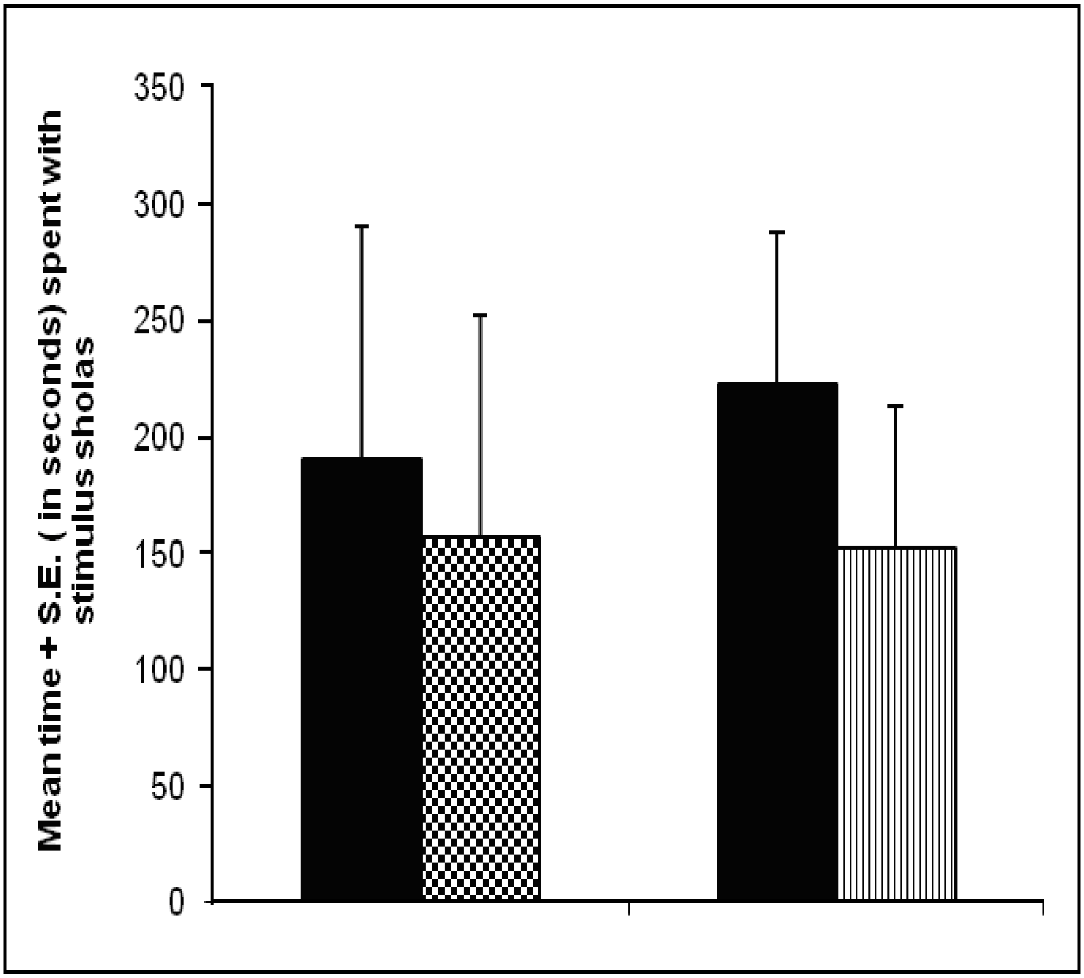


Figure 2. Preference of climbing perch for the shoal of unfamiliar conspecific ■ /familiar heterospecifics (30 days of familiarity; tilapia ▦ and Malabar mystus ▥);N=31.

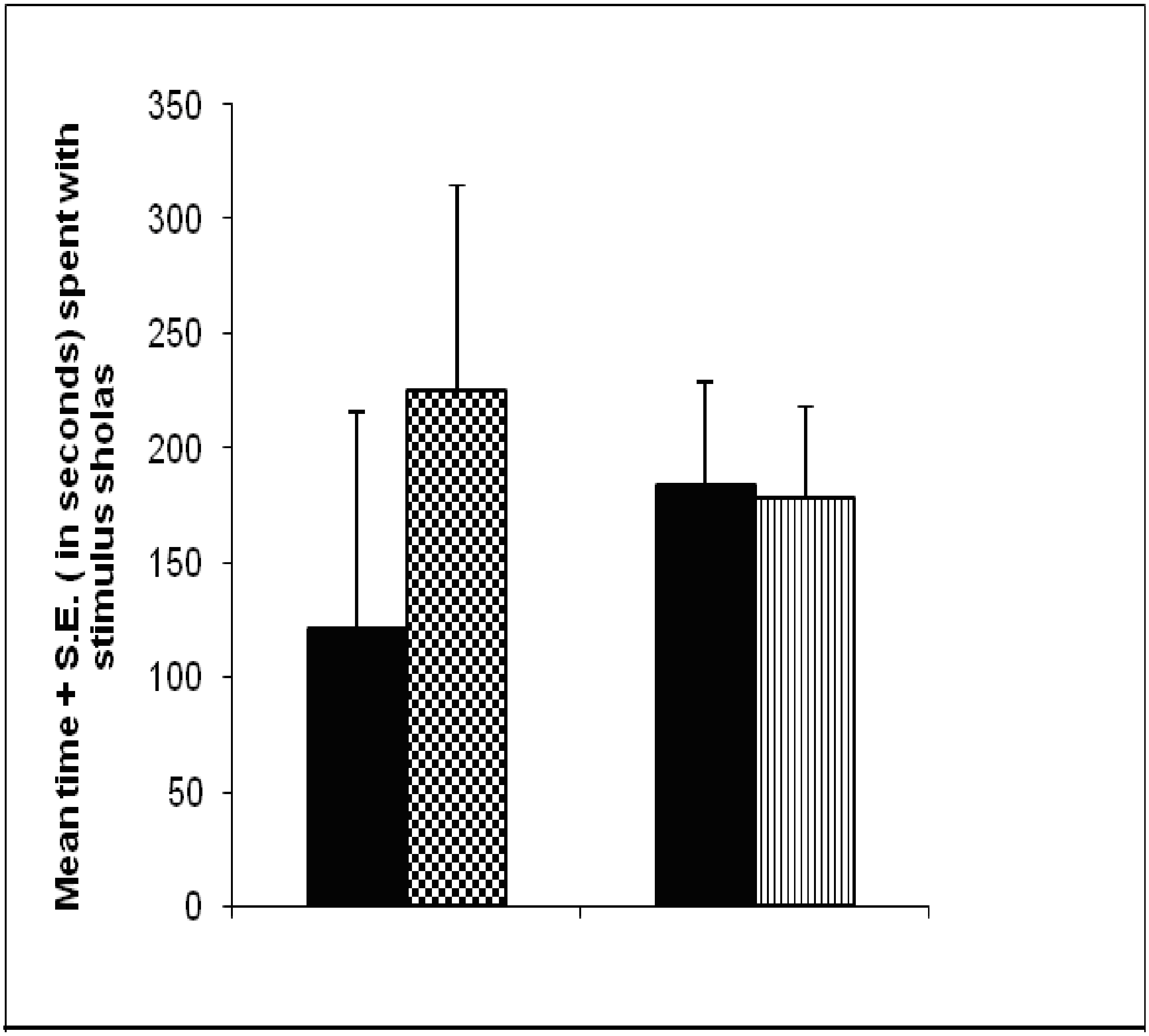


Figure 3. Preference of climbing perch for the shoal of unfamiliar conspecific ■ /familiar heterospecifics (90 days of familiarity; tilapia ▦ and Malabar mystus ▥); N=31.

DISCUSSION

The shoaling decision of climbing perch, when presented with equal sized shoals of unfamiliar tilapia or Malabar mystus, and unfamiliar conspecifics, were always biased towards the unfamiliar shoal of conspecifics. Present results indicate that the climbing perch prefer conspecifics to shoal with. According to Hoare and Krause (2003), preference for and joining of shoals of conspecifics are beneficial, as it facilitates the transfer of relevant acquired information within the group (Passive Information Transfer, P.I.T.) more effectively, as all members share diet preference, habitat requirement and face similar predation pressures with conspecifics than with heterospecifics.

Fishes gain maximum benefit of shoal life only if they are able to perform group manoeuvres effectively (Pitcher and Parrish, 1993). However, synchronized movement patterns are not easy to perform in mixed species shoals due to the variation in morphology and disparity in the behaviour patterns of member species. Thus, in a shoal composed of heterospecifics, climbing perch may have to face drawbacks of oddity effect (Landeau and Terborgh, 1986). The oddity effect describes that odd members in a group are more vulnerable to predation due to their conspicuousness in morphology and behaviour from rest of the members. This will attract the attention of predators to target and eye lock the unique member, thus reducing benefits of dilution effect and predator confusion gained by joining a large group (Pitcher and Parrish, 1993; Guthrie and Muntz, 1993). In nature, it can be seen that mixed species shoals usually segregate species-specifically to perform predator avoidance skills more effectively during predator attack (Wolf, 1985; Allan and Pitcher, 1986). The avoidance of odd individuals through passive or active exclusion is seen during parasitic infection, where the infected fish becomes conspicuous due to their inability to maintain swimming speed resulting from parasitic load (Barber *et al.* 2000; Hoare and Krause, 2003).

Synchronized performance of many behaviour patterns is vital for an obligatory air gulping fish like the climbing perch. These fishes surface frequently to gulp atmospheric air, a behaviour which makes them vulnerable to aerial predators. To reduce the risk of predation, members of a shoal surface in a synchronized manner. Orchestrated performance of air gulping behaviour induces confusion effect and unarms the predator to execute successful attack on a located single fish (Graham, 1997; Chapman and Chapman, 1994).

Recent studies show that climbing perch is able to develop familiarity with conspecifics and they can recognize individual members of a familiar shoal after getting experience for 14 days (Binoy and Thomas, 2004; 2006). However, the fish failed to exhibit any sort of preference based on familiarity with heterospecific shoals, even after living together for 30 days. The inability of climbing perch to exhibit preference for heterospecific shoal may be due to the incapability of the fish to acquire familiarity with heterospecifics. An alternate hypothesis is that the benefits obtained by shoaling with unfamiliar conspecifics may be greater than shoaling with familiar heterospecifics and hence the climbing perch ignored the shoal of familiar heterospecifics.

When the duration of familiarization was increased from 30 to 90 days (experiment 3), the climbing perch exhibited preference towards the shoal of familiar heterospecific tilapia. This result reveals that in climbing perch, the duration of experience required for the acquisition of familiarity with heterospecifics is longer than the time required for developing familiarity with conspecifics.

However, in climbing perch an experience of 90 days of living together was not sufficient for the expression of familiarity dependent preference towards another heterospecific species, Malabar mystus. Phenotypic oddity (Landeau and Terborgh, 1986) is the suspected reason behind the discrepancy in the ability of climbing perch to develop familiarity with a catfish having different morphological features. Here, it is important to note that the body of tilapia is laterally compressed like that of the climbing perch. Additionally, the feeding behaviour as well as the mode of locomotion of tilapia and climbing perch is very similar and difficult to distinguish while they move together. In contrary, Malabar mystus is a cat fish conspicuously different in morphology and the mode of locomotion from the climbing perch, due to its spindle shaped body with dorso-ventrally compressed head bearing feelers. Hence, the phenotypic and behavioral oddity might be one of the reasons for the inability of climbing perch to develop familiarity with Malabar mystus, even after 90 days of experience. These results suggest that the morphological uniqueness as well as behavioral oddity of heterospecifics can affect the acquisition of familiarity and influence the shoaling decision of climbing perch. The influence of the visual characteristics of heterospecifics on the development of familiarity may be further supported by the results discussed in Chapter III, which show that climbing perch relies more on the visual characteristics of conspecifics for the development of familiarity.

In summary, many studies report that the shoaling decision of a fish is influenced by the familiarity with the members of a stimulus shoal (Binoy and Thomas, 2004; Morrel *et al.* 2007). However, present study reveales that the acquisition of familiarity as well as its expression in the form of preference towards a specific shoal is a time dependant process, varying in accordance with the phenotypic characteristics of the stimulus species. The results of present study support the findings of Landeau and Terborgh (1986), which states that multi-species shoals may result when the antipredator benefits of membership to a large shoal outweigh the costs of phenotypic oddity. Hence, future studies using different species may provide better understating of familiarity trading off with phenotypic oddity.

Section summary

Familiarity and shoaling decision

In climbing perch, shoaling decisions are biased towards a familiar shoal or a familiar individual. However, given a choice between a large unfamiliar shoal and a small familiar shoal, climbing perch is seen trading off familiarity with size of the shoal in a decision making situation. It is possible that benefits enjoyed by the fish, while joining with a large shoal, outweigh the advantages of familiarity in several contexts. Unlike several other species, climbing perch primarily depends on the visual charecterisitcs of conspecifics or heterospecifics in assessing their identity during the familiarization process. The preference shown by the fish towards a shoal of tilapia and avoidance of a shoal of Malabar mystus indicates that, in climbing perch development of heterospecific familiarity is possible, only if the other species is morphologically similar to that of the conspecifics. Perhaps, the cost of conspicuousness in a group of heterospecifics with significant variation in morphology (the phenotypic oddity) and difference in behaviour dampens the expression of familiarity-dependent preferences and influence the shoaling decision of climbing perch.

Section II

Propensity to take a risky decision-the boldness

The boldness

Being the major component of aquatic food web, and being prayed upon by aquatic, aerial and amphibious predators, in teleost fish, decision making is a difficult task as there is no surety about whether one's choice will augment fitness or not (Milinski, 1993). However, on several occasions fishes are compelled to take risky decisions. The propensity to take a risky decision is defined as the boldness (Wilson *et al.* 1994). In fishes, boldness can vary from individual to individual as well as from context to context. In the view of Coleman and Wilson (1998), individuals of a fish population can be categorized into three sub-groups based on their predisposition to take risk: bold, intermediate and shy. Bold individuals tend to be risk takers and will quickly approach novel objects and explore novel environments. By contrast, shy individuals tend to be risk aversive and neophobic with behavioural responses often accompanied by fear response, such as freezing in a novel habitat (Brown and Smith, 1996; Budaev *et al.* 1999a; b; Templeton and Shriner, 2004). The 'intermediates' are placed in a position middle to the bold and shy individuals.

Though, the boldness is a flexible trait, there are standard methods for measuring the boldness of a fish (Brown *et al.* 2007). The major assays are focused on behaviours like tendency to inspect predators (Godin and Dugatkin, 1996), foraging under predation risk (Magnhagen, 2006), response to novel objects (Sundström *et al.* 2004), and open field test (Budaev, 1999a; b). According to Brown *et al.* (2007), measuring the latency to initiate the exploration of a novel area is now being accepted as the most recommended method of measuring the boldness of a fish.

Boldness is species specific

Gill and Andrews (2001) suggest that the boldness of a fish is correlated with species specific needs. These authors assumed that different species of fishes with difference in behaviour repertoire, adapted to different niche, exhibit variation in their inclination to take risky decisions. Recently, Yoshida *et al.* (2005) analysed species specific character of boldness by quantifying the latency to initiate exploration of a novel area by fishes. These authors compared the reaction of three species of fishes: bluegill sunfish (*Lepomis macrochirus*), crucian carp (*Crassius longsdorfi*) and gold fish (*Crassius auratus*), to a novel environment. The results indicate that the bluegill sunfish is boldest among the three species. The crusian carp was found to be the shyest and gold fish occupied a position in between the bluegill sunfish and crucian carp. Analysis of genetic relatedness revealed that gold fish is genetically closely related to crucian carp, but the domesticated life in artificial environment might have made them bolder than crucian carp. Therefore, Brown *et al.* (2007) suggested that the boldness is a species specific and genetically determined character and each species will continue to exhibit its inherited level of boldness until an external selection pressure acts on it

Genetic correlates of boldness

Iguchi *et al*. (2001) have demonstrated, using two cloned strains of red spotted cherry salmon (*Onchorhynchus masou macrostomus*), that boldness has a genetic basis. To add with this result, Brown *et al.* (2007) have shown that the boldness of first generation individuals of *Brachiraphis episcopi* was similar to that of their parents. This result supports the contention of genetic determination of the trait, the boldness-shyness continuum. Recently Vilhunen *et al.* (2008) have gone beyond just speculating genetic determination of boldness. These authors have demonstrated that genetically more variable individuals (mesaured as micro satellite heterozygosity) are more prone to take adventurous decisions under the risk of predation. Additionally, this association was significantly consistent over three populations with different backgrounds, suggesting that in this species boldness is correlated with heterozygosity. However, they failed to find any relationship between genetic variability and the degree of boldness, when threat from the predator (simulated using predator odour) was absent. These results reveal that the predation pressure can bring forward variation in genetic correlatedness of boldness in the long run of evolution (Vilhunen *et al.* 2008).

Boldness and mode of locomotion

As many studies measures boldness as the latency to initiate exploratory behaviour in a novel area, an act controlled by the motor system dedicated to the locomotor activity, Gill and Andrews (2001) analysed an interesting hypothesis: whether initiation of exploration of a novel area have any relationship with the mode of locomotion followed by the fish species. According to Westneat and Walker (1997), fishes can be divided into three groups based on their mode of locomotion: carangiform, sub-carangiform and labriform. Carangiform fishes follow stiffer, fast movements and they gain the force of propulsion by the rapid oscillation of the tail. Here, the majority of movements are concentrated in the very rear part of the body and tail (Westneat and Walker, 1997). The sub-carangiform mode of locomotion varies from carangiform in such a way that the majority of movements is concentrated on the rear half of the body, instead of the rear end of the body. In labriform mode, the propulsive force is generated by the oscillatory movement of the pectoral fin.

Gill and Andrews (2001) measured the exploratory activity of nine species of Caribbean reef fishes in response to their first encounter with a novel environment in a large aquarium. The result demonstrated that, regardless of the mode of locomotion, all species including territorial ones initiated the exploration of novel habitat. However, their boldness varied significantly in accordance with the mode of locomotion. The carangiform fishes were more shy compared to the other two types of fishes, and initiated the exploratory activity slowly and cautiously. Though, they were slow in the beginning of the trial, their activity level slowly attained a stable value as they became familiar with the novel environment. However, there was no significant variation in the exploratory activities of the sub-carangiform and labriform fishes. These results show that genetically determined mode of locomotion has profound influence on the boldness of a species.

Context specificity of boldness

Though, there are reports supporting the genetic control of boldness (Wright *et al.* 2003, Stein *et al.* 2001; McCune, 1995), many fishes show context specific variation in their boldness. For example, Coleman and Wilson (1998) have demonstrated that boldness exhibited by individual pumpkinseed fish (*Lepomis gibbsons*) varied significantly in presence of threatening stimulus (a red tipped meter stick) or a novel food source. Moreover, the fish that stayed still, rather approached or fled (could be considered as individuals with intermediate level of boldness), boldly foraged in presence of the predator compared, to the bold or shy individuals. According to Ward *et al.*

(2004b), reason behind this context specific variation of boldness is the options available to the fish, and each fish can initially decide whether to respond to a given stimulus and then behave in investigative or cautious manner. Thus, the fish showing an intermediate response to the threatening stimuli had simply chosen not to respond at all, in presence of a novel object (meter stick), but when confronted with an actual predator they responded boldly. This context specific alteration in the boldness is seen not only in fishes, but many other species like the big horn sheep (*Ovis canadensis*, Reale *et al.* 2000), Harris sparrow (*Zonatrichia querula*) and human beings (*Homo sapiens,* McCune, 1995) also modify their boldness depending on the context.

According to Salonen (2005), in European graylings (*Thymallus thymallus*), the boldness and its correlated factor aggression was found to be varying significantly in young ones produced from the same stock in two successive years. This author speculates that yearly changes in the atmospheric factors (which are yet to be discovered) present in different years might be considered as the suspected reason behind this unexpected result. Salonen (2005) continues her discussion by challenging the genetic control of boldness by putting forward the hypothesis that, even though, boldness has a genetic basis, it is fine tuned by the needs, niche and the quality of the habitat.

The conflict of opinion about the context specificity of boldness does not end up with the result obtained from European graylings (Salonen, 2005). Analysis of boldness exhibited by sticklebacks in four different situations challenged the context specificity of boldness itself. Ward *et al.* (2004b) showed that the boldness of a species is rather consistant and does not vary according to the context. In the light of the above experiments, Ward *et al.* (2004b) opines that rigorous experimental studies are needed for ascertaining context specific expression of boldness in fishes.

Age, size, metabolism and boldness

According to Brown and Braithwaite (2004b) boldness of a fish is correlated with its body size and metabolic rate. Sih, (1997) suggests that the nutritional status and the rate of metabolism can affect the motivational status of the fish, which in turn reflect in the expression of boldness. The enhancing effect of hunger on activity level and boldness has been demonstrated by Weiser *et al.* (1992) using cyprinids fishes. Theoretically, the metabolic rate increases with the natural log of body mass, but metabolic rate per gram body weight decreases with the increase in body size (Brown *et al.* 2005). In teleost fishes, the resting oxygen consumption and the natural log of body mass gives a scaling exponent of 0.79 (Clark and Johnston, 1997), meanwhile, in all other vertebrates metabolic rate per gram of body weight and body size has a negative exponential allometric relation. All these observations converge to the ‘metabolic hypothesis’ which states that juvenile fishes with higher metabolic rate during the growing age are more likely to take risky decisions than larger individuals (Brown and Braithwaite, 2004b).

Many studies show that the size of a fish is correlated with its age and smaller fishes can be considered as younger than the large fishes in a population (Brown and Braithwaite, 2004b; Dowling and Godin, 2002). Small fishes have lower body weight and fat reserve, higher drag coefficient and faster metabolic rate due to the growth than large fishes (Wooton, 1994; Krause *et al.* 1998; Skalski and Gillaim, 2002). Due to this increased need for the metabolites, they become hungry very fast and this increased level of hunger compels them to be bold and to emerge out from the shelter soon, as well as to try luck in front a predator. Hence, metabolic hypothesis assumes that young (small) fishes are bolder than old (large) fishes.

Though, many species obey the rules of metabolic hypothesis, it was found to be incorrect in poecilid *Brachyraphis episcopi* (Brown and Braithwaite, 2004a) and banded killifish (*Fundulus diaphanous,* Dowling and Godin, 2002). In banded killifish, the latency to emerge out from a refuge after the predator attack was found to be negatively correlated with the size and small killifishes spent more time inside the shelter, before emerging out, after the shock of a simulated predator attack (Dowling and Godin, 2002).

The metabolic hypothesis was challenged by 'predation hypothesis' which proposes that small fishes are more vulnerable to the predation compared to large fishes, and will exhibit reduced level of boldness by emerging slowly from the shelter than the large fishes (Sogard, 1997). Comparison of the rate of metabolism by measuring the RNA level of the bold and shy individual brown trouts with difference in their body size (and metabolism) also favoured the predation hypothesis, but not the metabolic hypothesis (Sundström *et al.* 2004). The result of this study confirmed that boldness is not correlated with metabolism (RNA level), and thus the size could not be considered as a predictor of boldness.

In order to handle this controversial context, Brown and Braithwaite (2004b) introduced two new hypotheses to support the late emergence of large fishes from the refuge provided. The first hypothesis states that, due to the increased exploratory urge and reduced level of fear towards the predator, the bold fishes will be eliminated in the earlier phases of their life by predation, and only the shy individuals might be surviving up to the older age (Brown and Braithwaite, 2004b). This assumption can be true in an aquatic ecosystem with very high pressure of predation and limited space available for the prey species to explore and escape. The second hypothesis postulates that, the length of a fish is correlated with its age and most of the old fishes inhabiting natural habitat are well aware of the danger caused by the predator, than the small, ignorant juvenile fishes. Hence, the large fishes take more time to recover from the fear and are cautious during the emergence from the shelter. More detailed discussions dealing with the relationship between size and boldness can be expected in the future.

Gender difference and boldness

Difference in the life history priorities lead to the differences in the behaviour of sexes including boldness (Jennison and Telford, 2002; Reznick *et al.*1993; 2001). In most of the species, male fishes are bolder than females (Brown *et al.* 2005). This elevated degree of boldness exhibited by the male fish is not easily influenced by external factors. For example, males of brown trout (*Salmo trutta*) never given any attention to the repeated predator attack and involved in the agonistic behaviour, even in presence of the predator (Johnsson *et al.* 2001). However, in comparison to the degree of boldness exhibited by males, female fishes are found to be shy and always hesitated to take risky decisions (Brown *et al.* 2005). In *Brachyraphis episcopi* males took less time to emerge out of a refuge and to engage in its normal activities (a sign of increased boldness), while females spent longer duration inside the shelter to reach a similar decision (Brown *et al.* 2005).

In the view of Brown *et al.* (2005), the proximate reason for the variation in boldness of male and female may be the variation in their hormone profile. The ultimate is the bolder male getting more chance of insemination and hence the enhanced fitness (Evans *et al.* 2003). Moreover, female fishes always prefer to mate with bolder males (Godin and Dugatkin, 1996). However, the increased level of boldness makes the male fishes short lived due to the vulnerability to predation, which increases hand in hand with boldness (Brown *et al.* 2005). This argument was found to be true in studies using *Poecilia reticulata*, where females stop feeding and concentrate more on antipredator tactics in presence of a predator while males will attempt for courtship in a similar situation (Evans *et al.* 2003; Reznick and Endler, 1981). So, it could be concluded that the males increases their fitness by making more insemination even under the threat of predation, while females increases their fitness by increasing the longevity by avoiding predators.

Brood and the boldness

The tendency to take a risky decision by a fish is very high during the period of parental care. The reason for this behavioural modification during the period of nest defence and parental care is the increased cost of shyness that has to be paid by the fish. If the fish hesitate to respond boldly in this critical period of reproduction, it will lose the fitness (Huntingford, 1976a;b). As a result, the nest defending three spined sticklebacks are bolder than its non breeding conspecifics, and the former will not desert the nest, when presented with an aquatic predator, the rainbow trout (*Salmo giardneri*, Kynard, 1979). These territory holding males will even go to attack the intruding males even under the threat of predation from the rainbow trout (Ukegbu and Huntingford, 1988). According to Pressley (1981), the boldness shown by a breeding male is positively correlated with the value of the brood being defended. This author established the hypothesis true, using sticklebacks and demonstrated that the boldness increases with the age of the fish and the number of eggs present in the brood. This study also revealed that the enhancing effect of brood on the boldness will decline as the breeding season reaches the climax (Ukegbu and Huntingford, 1988).

The bold fish learns more

The bold fishes are not only quick to make exploratory decisions, but also excel in learning various tasks (Brown *et al.* 2007). There are many studies revealing the association of boldness with different types of learning abilities of a fish. Sneddon (2003) using brown trout (*Onchorynchus mykiss*) model system demonstrated that the bold fishes learn rapidly the appetitive conditioning task than their shy counterparts (Sneddon, 2003). Additionally, Templepton and Giraldeau (1996) have shown that bold fishes are also equipped with higher level of latent learning ability, which makes their risky exploration of novel areas or objects worthful. This higher level of latent learning ability allows these fish to utilize the information learned during the exploration in a similar context without any reinforcement (Lieberman, 1990). The bold fishes are good social learners, and they gather more social information and achieve a dominant status in the shoal, which increases access to the biologically significant resources like food, mate etc., and make them a favourite choice of natural selection (Bumman *et al.* 1997).

Fuster (1985) binds the enhanced learning ability of bold animals with the increased activity of reticular arousal system (RAS) of the brain. RAS is a column of nerve cells extending to the cerebral cortex and thalamus from the lower parts of the brain. This system is provided with axonal connections to spinal chord also (Carlson, 1995). When an animal starts exploration, the RAS starts to show heavy activity. This high activity of RAS in association with heightened activity of eyes, increased alertness and intensity of attention, enhances the pace of learning process by increasing the ability of an organism to discriminate between objects quickly and reliably.

Boldness-aggression syndrom

The probability of taking a risky decision is positively correlated with the degree of aggressiveness exhibited by that individual (Höjesjö, 2002; Sundström *et al.* 2004). The relationship between these two characters is evident in cichlid *Nannacara anomala*, where bold individuals are more willing to display aggression and escalate it to agonistic interaction than their shyer conspecifics, both in presence and absence of a model predator (Höjesjö, 2002).

This correlation between aggression and boldness is known as aggression-boldness syndrome as these two traits are associated even at the individual level (Salonen, 2005). Accoding to Bell (2005), these two traits show much tight connection, so that it should be considered related to each other, both within and between populations. In the view of Tully and Huntingford (1987), the causative agent of the link between aggression and boldness is the fear induced suppression of ongoing behaviour, a common factor present in both situations. Many authors suspect that such a correlation could be the product of the genetic linkage among these two traits (Sokolowski, 2001; Van Oers *et al.* 2004) or owe to some underlying physiological constraints:for example an energy allocating trade-off, that is difficult to decouple or modify over evolutionary time (Sih *et al.* 2003, 2004). Moreover, this correlation between boldness and aggression was found to be constant and is not at all affected by the variation in environmental quality. Although, the boldness of a species may be altered due to the early life experience, its association with aggression is maintained (Salonen, 2005). Furthermore studies of Salonen (2005) validate that the boldness changes with aggression hand in hand and the link between these two vital traits is not affected by the absence of selection force (e.g. lack of predator or cues announcing emergency) in the due course of development.

The association between boldness and aggression has ecological as well as evolutionary advantages (Sundström *et al.* 2004). The bold fish takes risk of the exploration of unfamiliar habitat due to their increased urge for exploration. This adventurous exploration is beneficial, as the unfamiliar habitat could provide the bold fish with more food due to lesser level of competition from conspecifics. This hypothesis is validated by the study of Wilson (1998), using pumpkin seed sunfish (*Lepomis gibbsons*). This author demonstrated that, bold individuals feed sooner in the laboratory their shy conspecifics, and they also had more food in their stomach upon capture in the wild. However, the exploration of unfamiliar area can be lethal due to the lack of knowledge about refuges, nature and tactics of predators present in the new region.

When the competition increases in a population, the shy individuals are also compelled to elevate their boldness in order to find new food sources by exploring new areas. As many fish species monitor and copy the behaviour of other individuals, the shy fishes will follow the route of bold fishes and will try to intrude into the new territory established by the bold fish (Höjesjö *et al.*1998; Johnsson and Åkerman, 1998; Brown and Laland, 2003). If the cost of taking risk of exploring a new habitat and time and energy lost in establishing a territory are to be compensated, the bold fish should defend its profitable territory. In this context, if the bold fish fail to exhibit aggression and dominance, they will be easily replaced by other fishes. Such a cost paid by the bold fish will not be favoured by natural selection, and these individuals will be eliminated from the evolutionary race. Consequently the correlation and inheritance of the boldness in combination with the aggression is a must for the survival of the bold fishes (Sundström *et al.* 2004; Abrahams and Dill, 1989).

According to Wilson (1998), the inheritance of behaviours in combinations is preferred by natural selection and hence it is adaptive. However, the adaptive value of this combination of behaviour will be different in different ecosystems, as each ecosystem harbours different types of predators (Price and Langen, 1992; Wilson, 1998; Sih *et al.* 2004; Bell, 2005). Price and Langen (1992) point out that such inheritance of behaviour could be maladaptive due to the expression of a trait only due to the compulsion to inherit and express in combination in a context where it is of little adaptive significance. For instance, the defence of territory by bold fishes will be costly in a homogenous environment as well as in areas with unpredictable food resources. Moreover, the cost of exploration will further increases if the fish tries to explore unfamiliar environment only due to its elevated boldness and curiosity, though an equal amount of resource and benefit is present in the familiar and non risky habitat (Abrahams and Dill, 1989).

Boldness in a shoal

Most of the prey fish species living under the threat of predation: practice two strategies to avoid the predator; either they invest more energy for vigilance (Krause and Ruxton, 2002) or they join a shoal by paying the costs of competition (Neil and Cullen, 1974). Though, the position of an individual in a shoal is flexible, different spatial position provides different levels of advantages like access to the food resources and rescue from the predators. As far as the success of foraging is concerned, the most appropriate position for a fish is in the front part of the shoal, at the same time, the vulnerability to predation is also at the maximum in this position (DeBlois and Rose, 1996). According to Bumman *et al.* (1997), leading position of a shoal is always occupied by the bold individuals enjoying a dominant rank in the group. This prominence and front position in a shoal compensate for the higher vulnerability to predation by providing greater chance for encountering and to get control over the food materials.

According to Ward *et al.* (2004), as the effective antipredator mechanism and active resource pursuit are mutually exclusive, bold fishes are interpreted as risking predation for increased resources (Sih, 1997; Wilson *et al.* 1994). For instance, sticklebacks that recovered rapidly after a shock of predator attack exhibited an increased rate of growth and always displayed a reduced tendency for shoaling. Moreover, if these fishes join a shoal, they always occupy a dominant position. In European wrasse (*Symphodus ocellatus*), individual fishes with the weakest shoaling tendency had the highest level of locomotion and a heightened level of spatial exploration ability (Walsh and Cummins, 1976). By contrast, the shy wrasse with higher shoaling tendency spent more time in performing antipredator tactics like freezing, due to the elevated level of stress or fear in a novel environment (Budaev, 1997; Walsh and Cummins, 1976).

The behaviour of the fish occupying the leading position of a shoal can affect the shoal dynamics and synchronized activity of other shoal members (Bumman and Krause, 1993). This is because the followers just copy the behaviours of the leading dominant individuals in a shoal (e.g. roach *Rutilus rutilus* and stickleback, Bumman and Krause, 1993).

Boldness and habitat quality

In nature, different areas of a large aquatic habitat show much variation in pysico-chemical as well as biological properties that it can be divided into microhabitats with different levels of selection pressures. Hece, only the fishes equipped with flexibility in behaviours and high level of adaptability can live and reproduce in a wide variety of environments. However, the variation in behaviour with reference to the ecological quality of habitat reflects in the boldness-shyness continuum of populations of a species originated from different environmental conditions (Brown and Braithwaite, 2004a).

The major ecological parameters affecting the boldness of a fishes are food availability, foraging competition, distance to be travelled to obtain the food (Dowling and Godin, 2002; Godin, 1997; Sih, 1997; Lima and Dill, 1990). According to Brown and Braithwaite (2004a) the predation pressure can modify many types of cognitive abilities of the fish. This assumption was found to be true in the case of boldness also (Brown *et al.* 2007). Many studies support the idea that fishes from an area of lower risk of predation show high level of boldness and they emerge from the shelter soon after a frightening experience (Pitcher and Parrish, 1993). These findings support the theory, that predator allopatric population of fish is less likely to respond fearfully to predators than the predator sympatric population (Pitcher and Parrish, 1993).

However, the relevance of this theory has been questioned by the experiments in *Brachyraphis episcope* collected from habitats with different levels of threat from predators (Brown *et al.* 2005). This study demonstrated that fishes from the areas of increased pressure of predation exhibit lesser level of shyness and they emerge out from the shelter sooner than the fishes collected from areas with lower risk of predation. The fishes from the areas with increased risk of predation cannot wait for a long time in a refuge, because these fishes expect predator at any moment in their home range. Moreover, for an individual inhabiting such a habitat, encounter with predator is not a rare event, and the fishes have to search for food and mate in the shadows of unpredictable predator attack. Hence, the prey species living under the risk of predation are well equipped with the tactics to escape from predators.(Brown and Braithwaite, 2004a).

A second proposition based on metabolic hypothesis is also available to explain the increased level of boldness exhibited by the fishes collected from habitat with high level of predation pressure (Brown *et al.* 2005). It is stated that fishes leading sympatric life with predators get only reduced access to food, that they seldom reach satiation. It is the hunger that compels them to emerge out of the shelter soon to compensate the metabolic needs.

Application of boldness for the welfare of the fish

Usually the fishes born and brought up in a homogenous environment of the hatchery exhibit converged and increased level of boldness due to the absence of spatial complexity and lack of predator stimuli (Salonen, 2005). Usually, induced bred larvae reared in artificial hatcheries, a habitat with extreme levels of homogeneity, are used for restocking and reintroduction of endangered fish species. As these fishes have no experience with predators, they are bolder than fingerlings developed in the natural environment. Thus these bolder individuals can become a threat to local population when released in to the natural water bodies (McMichael *et al.*1999). The bold newcomers with increased aggression and dominant status will get hold of the biologically significant resources like the food and mates soon after their entry in to the new area. This problem becomes further complicated as female fishes prefer bolder males to mate with (Godin and Daugatkin, 1996). As a result less aggressive native fishes will loose their territories and ultimately their fitness (McMichael *et al.*1999; Einum and Fleming, 2001).

The inflow of bold fishes will, not only affect the equilibrium in an existing population but also alter the genetic composition of existing population, since boldness is inherited. Ultimately the immigration of genes for elevated boldness will lethally affect the resident fish population (Koskinen *et al.* 2002; Susnik *et al.* 2004; Madeira *et al.* 2005). Hence, the knowledge about the boldness of the individual fish species living together in a habitat is an important factor to be considered, while developing strategies to restock and reintroduce endangered species (Brown and Day, 2002; Brown and Laland, 2001).

However, the increased fitness of bold individual is a short lived phenomenon as the risk of predation increases hand in hand with boldness (Salonen, 2005). According to Brown and Day (2002), the bold individuals will even go to explore predators and unfamiliar areas where danger is unpredictable. As a result, most of the bold fishes will be eliminated from their habitat due to the increased curiosity, exploratory urge and aggression; the behaviours that helped them to get control over the resident conspecifics. This reduction in the survival due to the increased boldness has been highlighted by the study of Olla *et al.* (1998). Their study shows that, hardly less than five percent of reintroduced young fishes reached adolescence. Hence, the fluctuation in the boldness of individuals inhabiting an ecosystem can make the population unstable (Brown and Laland, 2001).

Study on the development of boldness using European graylings (*Thymallus thymallus*), that are reared in a homogenous environment in hatchery, gave a contradictory result. In this species, the fishes reared in a homogenous condition exhibited a reduced level of boldness compared to their counterparts collected from the natural water bodies (Salonen, 2005). However, the reduction of boldness is as lethal as elevation of it during the restocking and reintroduction, as the shy naïve fishes cannot withstand the pressure of competition from the resident individuals. Hence, the elimination fishes before reaching the phase of reproduction will badly affect the success of re-introduction programme itself (Miller *et al.* 2004).

Applications of data analyzing the boldness of a species are used in sea-ranching (Sundstorm *et al.* 2004). In sea-ranching, fish larvae are collected from the field and reared up to a certain size in artificial conditions, and then released into the wild with the hope of significantly reducing larval mortality. For example, youngones of brown trout are collected and kept for the first two years in artificial conditions, before placed back in to sea (Sundström *et al.* 2004). The alteration in the boldness due to this early life experience in a homogenous environment can affect the success of sea ranching programme (Sundström *et al.* 2004).

A recent study by Salonen (2005) shows that the degree of flexibility in boldness required to survive successfully varies in accordance with the characteristics of the ecosystem. For instance, European graylings (*Thymalus thymalus*) inhabiting the lotic water of rivers are bold and aggressive compared to the pond dwelling conspecifics. This variation is evident in the boldness of young ones produced from the parents collected from lentic and lotic ecosystems (Peuhkuri and Salonen, 2004). Additionally, the boldness of the young ones produced by the cross breeding between parents collected from different ecosystems is unpredictable. Hence, Salonen (2005) suggests the use of progenies produced from parents living in ecosystems with properties similar to that of the water body proposed for the restocking.

Even though the variation in boldness is not a desired condition during the reintroduction programs, these young fishes could be trained to attain a desirable level of boldness, before introducing them in to the natural water bodies (Sneddon, 2003). Recent works demonstrate that, if kept in an environment with spatial complexity or maintained with variation in the availability of food materials, the hatchery reared shy cod (*Godus morhua*) larvae will become bolder and grow fast. Such larvae are better learners compared to their conspecifics reared in a homogenous habitat and will quickly locate shelters and take refuge very fast in response to a predator attack. This enhanced learning ability helps them to adapt quickly to the spatial complexity of the natural ecosystem in which they are introduced (Braithwaite and Salvaness, 2005). Moreover, fishes with experiences in a complex habitat will easily shift to the new menu available in the natural habitat, ability absent in shy fishes born and brought up in the homogenous habitat with constant food availability.

Braithwaite and Salvaness, (2005) postulates that the increment in the boldness and correlated negative impact on the antipredator behaviour and survival of the fishes resulting from long term stocking in the captivity can be reduced by making variation in the spatial properties and food availability. Hence they expect a new system of bio-manipulation for the management boldness and allied behaviours, to increase the success rate of reintroduction programmes and the sustainable maintenance of the existing fish stocks.

Chapter I

Evaluation of the effect of repeated exposure on boldness

INTRODUCTION

The urge to explore a novel area or novel object is a part of behavioural profile of all most all animal species (Crusio, 2001). However, exploration of a novel area is dangerous as the explorer is unaware of pitfalls present in such an environment, while the same behaviour helps to find new food sources and escape routes (Sundström *et al.* 2004). The bold individual will exhibit a quick initiation of exploration and active search of a novel area, while the shy or emotional ones show less interest for exploration and take more time to start locomotory activity and exploration (Crusio, 2001). The 'intermediates' are put in position middle to the bold and shy individuals (Coleman and Wilson, 1998)

The exploratory activity and boldness of animals always fascinated the scientists. The earlier attempts for the scientific quantification of these behaviour patterns comes from the studies of Hall (1901 quoted in Silverman, 1978) using rats. The trendiest version of apparatus used for analyzing different aspects of boldness and other behaviour patterns connected with exploratory behaviours is known as 'open field*'*. This apparatus is a well illuminated homogenous open area without any complexity. Here, the focal animal is introduced in to the well-lighted central arena of the open field, and activity of the animal is recorded and quantified, either manually or using electronic devices

(Silverman, 1979). The bold (less emotional) animals visit the bright lit area soon after the entry in to the apparatus. By contrast, the shy (emotional) animals show latency to move around and prefer the areas with lower luminescence to focus the searching activity. The duration of the behavioural measurement in open field also varies (Crusio, 2001): some authors study the activity only for a few minutes (Flint *et al.* 1995), while others observe the animal for twenty minutes or more (Foshee *et al.* 1965). Survey of literature reveals that, circular open field with bright inner sides and floor marked in segments to quantify the locomotor activity is the most popular version (Siverman, 1978). Nowadays, open fields of different shape and size are used according to the species and hypothesis tested (Crusio, 2001).

Even though, the open field apparatus is widely used even now to measure the exploratory activity and boldness, many authors question the validity and usefulness of the data obtained from this apparatus (Archer, 1973; Walsh and Cummins, 1976). The ambiguity in interpreting the behavioral response in an open field arises partly from the open field situation itself, where animals are forced to explore the novel environment. In such a situation, the effect of compulsion cannot be separated from the boldness (Yoshida *et al*. 2005). Hence, many researchers studying exploratory behaviour and boldness of animals preferred another apparatus named *run-way apparatus*.

The run-way apparatus consists of a shaded start chamber and an illuminated straight runway (Fujita, 1984). The runway is separated from the start chamber by a guillotine door. The shaded start chamber serves as a shelter, where the emotional or shy animal can stay away from all the external stimuli. Additionally, the shaded ceiling of the start chamber increases the refuge value of the start chamber (Yoshida *et al.* 2005). The data obtained from using run-way apparatus for measuring boldness is considered to be more precise, as the decision to explore or hide is left to the animal (Fujita, 1984; Fujita *et al*. 1994), a condition which is not possible in open field apparatus. Hence, the shy animals are seen staying longer inside the start chamber of run-way apparatus than the bold animals (Brown *et al.* 2007).

The trend shift from the open field apparatus to the run-way apparatus is also reflected in studies using fish model systems (Yoshida *et al.* 2005). The exploratory behaviour and boldness of the fishes are being quantified using aquatic version of open field apparatus. Here, the well lighted aquarium (with all the specification of open field apparatus used for testing terrestrial animals) filled with water up to the level required for the free movement of the focal fish, called *swim-way* apparatus is used (Warren and Callaghan, 1976; Gerlai, *et al*. 1990; Gerlai and Crusio, 1994).

The fish exhibit behaviours like freezing, reduced locomotion, startle response or hyperactivity in a novel environment (Russel, 1967a; Yoshida *et al.* 2005). For example, the guppy (*Poecilia reticulata*) showed startle responses and rapid swimming around the tank when introduced into the unfamiliar experimental arena inside the open field apparatus (Russel 1967a, b). By contrast, the crucian carp has taken a longer latency (of 17± 3.63 minutes) to initiate the exploratory activity (Yoshida *et al*. 2005). The basis for the hyper reactivity in a novel environment may be the fear evoked by the novelty itself. This fear initiated hyperactivity can affect the quantification of boldness as the separation of initial startle response from the boldness-dependent initiation of exploration is very difficult (Yoshida *et al*. 2005). The situation becomes further complicated in the light of the study using paradise fish (*Macropodus opercularis*) model system, which revealed that the fishes will show high level of startle reactivity and movements when handled by the human beings (Davies *et al.*1974).

The influence of neophobia and hyperactivity can be controlled effectively by habituating the focal fish with the experimental arena by giving repeated exposure (Yoshida *et al.* 2005). The attenuation of hyperactivity through familiarisation with novel experimental arena was unequivocally demonstrated by Gomez-Loplaza and Morgan (1991). These authors have demonstrated that the isolated angelfish, (*Pterophyllum scalare*) decreased its hyper activity as the time spent in the novel area increased.

The present study is designed to investigate the response of climbing perch in a novel environment and to quantify its boldness by estimating the latency to initiate the exploration of a novel area in an open field situation. The scope of this study also includes the quantification of variation in boldness in response to the experience (repeated exposure) with the unfamiliar environment.

Apparatus

Boldness of the climbing perch was analysed using an apparatus developed by combining the characteristics of open-field and the swim-way apparatus (Binoy and Thomas, 2003). Apparatus consists of a rectangular aquarium with a start box (Fig. 1). An aquarium (60 x 32 x3 2 cm) was divided into two chambers, A (20 x 32x 32 cm) and B (40 x 32 x 32 cm) with transparent acrylic sheets. An enterance (8 x 4 cm) was provided in one corner of the partition wall. Three sides of the aquarium were covered using black paper to reduce the external interference. Differing from the swim-way apparatus, here the partition between the start box and the swim-way was made using a transparent acrylic sheet with an enterance. In this apparatus no guillotine door was used and the cover on the ceiling of the start chamber was also avoided to reduce the refuge value of the start chamber.

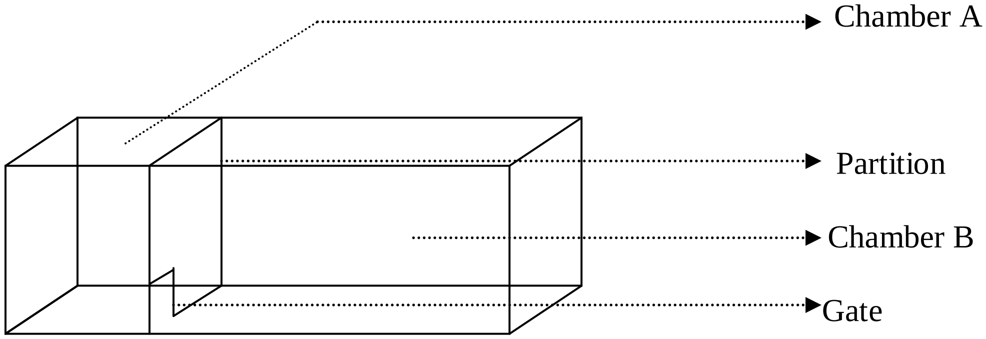


Figure 1. Diagramatic representation of the apparatus used to study the boldness of climbing perch.

Testing the boldness

The focal fish was introduced individually into the chamber A, and the latency to initiate the exploration of chamber B, was recorded. The initiation of exploration is defined as the time taken by the fish to come out of the Chamber A, through the enterance provided. After coming out of the chamber A, the focal climbing perch was given five minutes for the exploration of chamber B. If any fish failed to come out from chamber A after 6 minutes, the trial was terminated and the fish was allocated a ceiling value of 360 seconds. Focal fishes were returned to its home tank, and tested using the same procedure on the next day. This procedure was continued for the five consecutive days. 28 individual climbing perch were tested as mentioned in the procedure. Fish once tested in an experiment was never used again. A compact fluorescent lamp (20w) on the top of the assembly lighted the apparatus, and all observations were made sitting behind a black screen with slits. All fishes were released back in to the site of collection after the experiment.

RESULTS

Analysis of the latency to initiate exploration of a novel area for five consecutive days using Kruskal-Wallis test has revealed that, in climbing perch boldness enhanced concomitantly with the experience in a novel environment (χ^2 = 73.873; N= 31; $P<0.001$, Fig. 2).

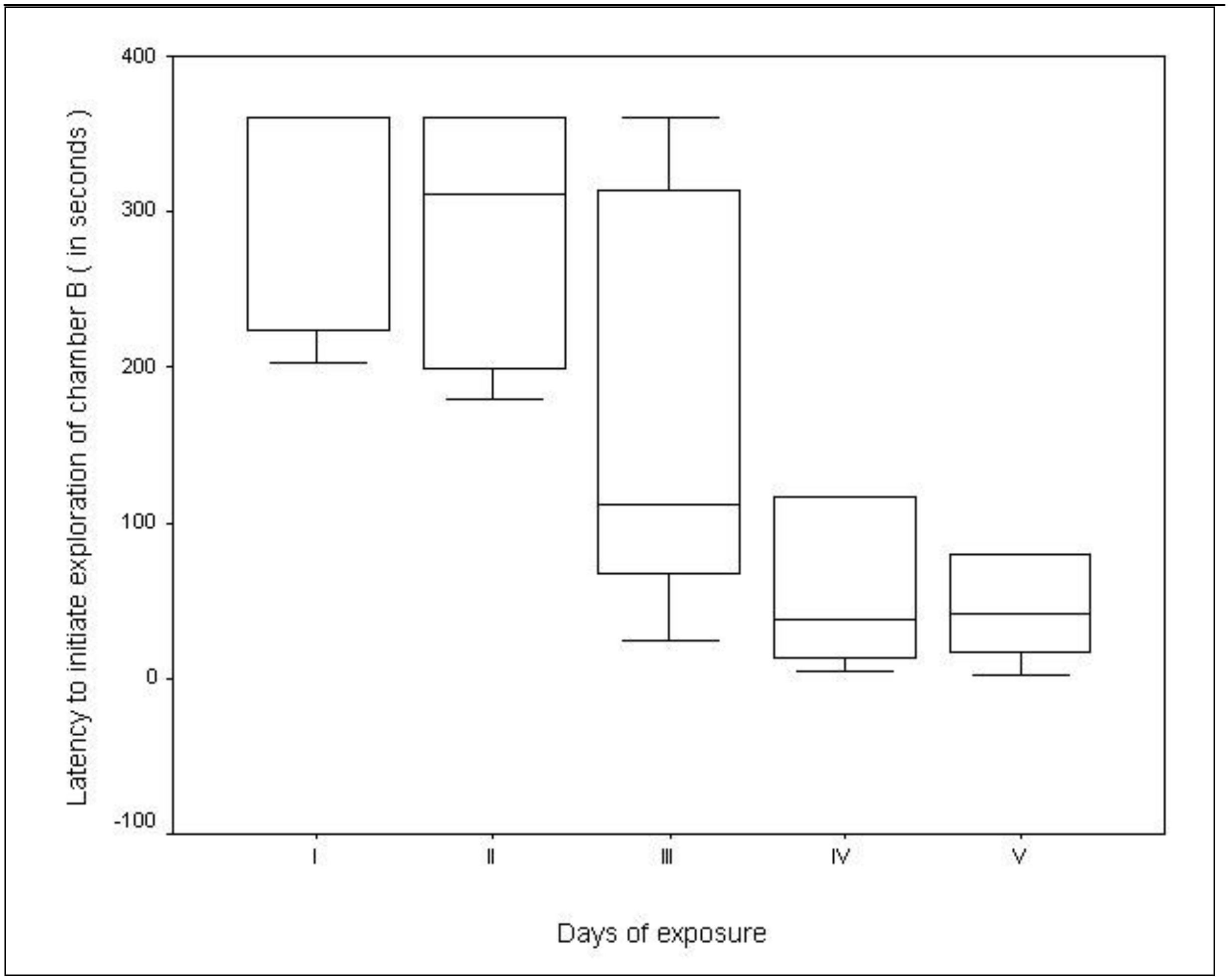


Figure 2. Variation in the boldness of climbing perch in response to the repeated exposure in a novel environment for five consecutive days.

DISCUSSION

On the first day of exposure to the novel environment inside the apparatus, the majority fish spent a short period inside the start chamber, afterwards they slowly initiated the exploration of chamber B. However, a minority of individuals (less than 5% of total number of individuals tested), did not show any interest to explore chamber B and spent whole test period inside the chamber A. Usually the fishes introduced into a novel habitat exhibit startle response and enhanced level of locomotor activity due to the fear evoked by the novelty (Gomez-Laplaza and Morgan, 1991). The other responses seen in the novel area are staying motionless or initiate the exploration after a long period of latency (Crusio, 2001). Interestingly, the initial startle response and enhanced locomotor activity reported in other fishes (Fujita, 1994; Yoshida *et al.* 2005) were not found in climbing perch. Instead, this fish exhibited a gradual increase in the locomotor activity as the days of exposure proceeded. Hence, it could be assumed that, such a reduced level of initial startle activity may either be a species specific characteristic or might have resulted from the presence of the start chamber (Chamber A) near the open swim way. Utilization of start chamber of the apparatus as a refuge in presence of any fear evoking stimulus by climbing perch is already reported by Binoy and Thomas (2003).

Borwn and Braithwaite (2004a) states that predator sympatric population of *Brachyraphis episcope* were bolder and reached a quick decision to explore a novel habitat compared to their conspecifics collected from an area with reduced level of predation pressure. Brown *et al.* (2007) states that such a variation in the boldness of predator allopatric and predator sympatric population is due to the variation in the degree of exposure to the predator during the course of life. Young sticklebacks chased repeatedly by their father were bolder than their siblings without such experience (Tully and Huntingford, 1987), thus, the exposure to a situation simulating predator attack during the early phase of life is an unavoidable factor, as far as the development of boldness of a fish is concerned. Hence, it could be suggested that having a sympatric life with various types of aquatic predators during different phases of life in its tropical aquatic habitat might have resulted in the enhancement of boldness in climbing. In such habitats with high pressure of predation, the hyperactivity may be lethal to the fish as the agile fishes will attract attention of the predators. Hence, climbing perch starts exploration cautiously and avoids the startling response and hyperactivity.

Reduction in the degree of responsiveness towards a stimulus after getting familiarity with it (often referred as habituation), has been reported in almost all animal species. Brown (2001) has reported such an influence of repeated exposure on the behaviour of rainbow fish. The rainbow fish performed antipredator activities more effectively and enhanced the success rate of escape response, as they became familiar with the environment. The boldness of the climbing perch was also found to be sensitive to repeated exposure and the latency to reach a risky decision of exploring a novel area reduced gradually as the familiarity with the environment increased. The latency to initiate the exploration of chamber B reduced dramatically from 360 to 42 seconds on the fifth day of exposure. Therefore this species can be used for tracing out the neural mecanihsm behind the positively correlated elevation of boldness with the familiarity, acquired as a result of repeated exposure to a novel habitat by a fish species. Hence, climbing perch offers an excellent model system to study biological, behavioural and neurobiological basis of boldness.

Chapter II

Taking risky decisions in presence of a predator or predator cues

INTRODUCTION

The fishes are considered to the excellent cost-benefit analyzers, taking only the decisions beneficial to enhance their fitness (Hart, 1993). However, none of the fish is able to take only beneficial decisions, as the web of life is too complex in natural habitats due to the multilevel inter and intra specific interactions and competition. In the due course of life, most of the fishes will have to face challenging situations frequently and only those fishes who dare to face threat by taking risky decisions can enhance the fitness in natural habitats (Godin and Davis, 1995).

The risky situations are always associated with fear. Johnes (1997) defined fear as a psycho-physiological response and phenomena, which act as a powerful motivation to evade threat. In fishes, fear has been characterized through freezing response (Brown and Smith, 1996; Budaev *et al.* 1999 a, b; Templeton and Shriner, 2004), increased branchial activity (Chandroo *et al.* 2004) etc. In a frightened situation, the total physiological condition of a fish will be altered due to the excessive production of hormones involved in the management of emergency. As far as fishes are concerned, predator is one of the most important sources of fear (Vilhunen *et al.* 2008). Consequently, Brown *et al.* (2005) states that, in presence of a predator, making a decision after assessing the cost and benefit by a prey fish species may show significant variation in the latency and its translation in to action. Additionally, Brown *et al.* (2007) validated this hypothesis by demonstrating that fishes born and grown in habitats with different levels of predation risk, shows variation in their ability to take a decision in a challenging situation. Their study shows *Brachyraphis episcopi* collected from an area of higher risk of predation exhibited higher disposition to take challenging decisions, compared to their conspecifics living in areas with lower risk of predation.

Different fish species sense the threat of predator by perceiving different cues emitted by the predator. Some species utilizes visual characteristics of the predator for the recognition (Hartman and Abraham, 2000), whereas, others depend upon the odour of the predator or the chemical cues present in the diet of the predator (Brown *et al.* 2000a). On sensing such cues the fish will shift to antipredator behaviours, which may vary from the refuge seeking and total avoidance of the area where threat is present (Dowling and Godin, 2002), to intense inspection of the areas where alarm cues are present (Brown, 2003). Some other fishes may take extremely audacious decision of inspecting the predator to understand its motivational status (Kelley and Magurran, 2003). For example, the banded killifish (*Fundulus diaphanous*) and the three spined stickleback (*Gastrosteus aculeatus*) took more time to take a bold decision of leaving the refuge on the detection of the presence of an aquatic or aerial predator (Dowling and Godin, 2002, Krause *et al.* 1998). On the other hand, species like *Poecilia reticulata* or *Cichlasoma nigrofasciatum,* exhibited increased predator inspection on sensing the presence of the predator (Brown, 2003).

In addition to the predator odour, and the chemicals present in the faecal matter of the predator, a third type of chemical cue which can initiate fear response in a fish is hypoxanthine-3N-Oxide (H_3NO), the putative ostariophysan alarm pheromone (Brown *et al.* 2000b; 2001; Smith, 1999). This chemical is present inside the skin cells of the fish and is released in to the water from wounds as an announcement of emergency to others (Brown, 2003). According to Brown (2003) these chemicals possess the power to escape digestion, and being present in the fecal matter of predator, can communicate the threat not only to conspecifics, but also to the heterospecifics. However, Korpi and Wisenden (2001) have demonstrated that, in many cases the exposure to alarm pheromones alone cannot initiate the fear response, but a combination of alarm pheromone with other characteristics of predator can induce fear in fishes. For example, zebra fish, which never exhibited any sign of fear on exposure to the conspecifics skin extract, displayed antipredator behaviour, when presented with a combination alarm chemicals and live aquatic predator (Korpi and Wisenden, 2001).

In many cases, exaggeration of certain morphological characteristics of predator can induce or enhance the fear response in prey species. The features like presence of large eyes, position of the mouth, and the movement of predator model can induce fear and initiate anti-predator behaviours in many prey fishes (Guthrie and Muntz, 1993; Karplus *et al.* 1982). For example, in paradise fish (*Macropodus opercularis),* degree of the expression of the anti-predator behaviour is positively correlated with the eye size of the predator model (Altbäcker and Csányi, 1990).

Many authors point out that, not only the presence of predator but also the presence of novel objects in the habitat can also influence risk taking tendency of the fish (Fraser *et al.* 2001).Coleman and Wilson (1998) have shown that the presence of a novel object like a red coloured meter stick in the habitat can influence the boldness of the pumpkinseed sun fish. Chapter II of this section analyses the ability of climbing perch to take a risky decision in various contexts shadowed with fear of predation.

MATERIALS AND METHODS

Apparatus

All experiments were conducted in an aquarium (60 x 32 x 32 cm) partitioned with transparent acrylic sheet into two chambers: 'A' (20 x 32 x 32 cm) and 'B' (40 x 32 x 32 cm; Fig.1). A guillotine door (8 x 4 cm) was provided in one corner of the partition wall. Washed fine river sand spread on the bottom of the tank acted as the substratum, and water level was kept at 28 cm. A compact florescent lamp (11 W) on the top of the assembly lighted the room and observations were made from behind a black screen with slits.

General procedure

Normally, when a fish is introduced into the chamber A of the apparatus, it will start moving inside the chamber within a short duration and will extend the exploratory activity to the chamber B, passing through the gate provided. The time taken by the test fish for the initiation of exploration of chamber B was taken as the measure of trading off neophobia with the decision to explore (Yoshida *et al.* 2005) and shorter period of latency to enter the chamber B, is assumed to indicate greater level of boldness and vice versa. The latency of initiation of exploration is defined as the time taken by the test fish to come out of chamber 'A' through the gate provided. If the fish failed to emerge from the chamber A after 6 minutes, the trial was terminated and it was allocated a ceiling value of 360 seconds. Each experimental fish was given seven minutes daily for four consecutive days to make it familiar with the apparatus and to avoid the error resulting from handling and the hyper reactivity in novelty (Russel, 1967a;b; Gomez-Laplaza and Morgan, 1991). The data obtained in these days were not taken for analysis.

On the fifth day of exposure all most all fishes reached chamber B within 42.5 seconds (median). This value is taken as control (I). 28 individual fishes were used in each experiment and none of the fish was used more than once in any experiment.

Experiment I*: *Aerial predator

In order to study the influence of the presence of an aerial predator on the boldness of the climbing perch, a stuffed crow (*Corvus splendense*) was used as described by Milinski (1993) and Krause *et al.* (1998). The stuffed bird was fixed on the partition wall of the apparatus in such a way that, the shadow of the bird fell near the gate.The test fish introduced in the chamber A had to cross the ‘predator above’, in order to reach the chamber B.

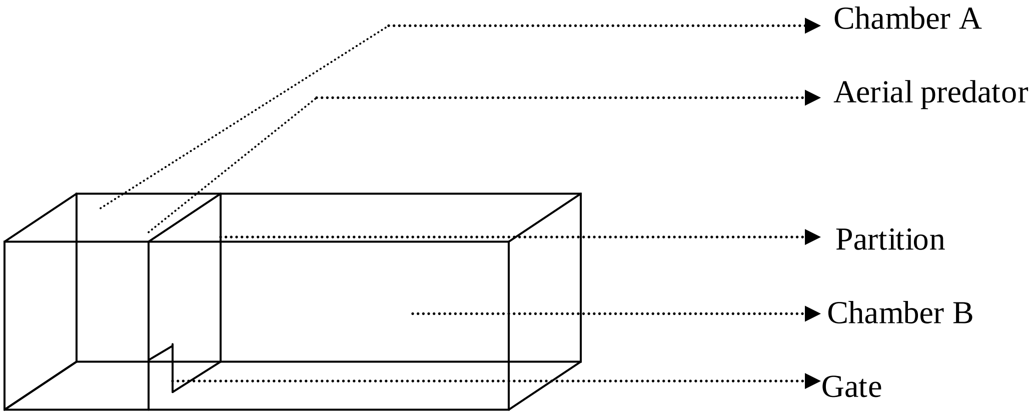


Figure 1. Diagrammatic representation of the apparatus used for studying the influence of aerial predator on the boldness of climbing perch.

Experiment II: Odour of aquatic predator

The mucilaginous skin secretions of the most common predator of climbing perch, striped murrel (*Channa striatus*) was used for testing the effect of predator odour on the boldness. To extract the odour producing skin secretion, murrels (of size 20±2 cm S.L. ± S.E.) were kept individually in 5 litre of water in a bucket for 12 hours. Mucilaginous skin secretion was extracted from 7 individual fishes and the secretion from each fish was filtered and stocked in separate air tight bottles inside the refrigerator until it is used.

One litre of water containing skin secretion of the aquatic predator was mixed with the water in chamber B, after closing the door. The door was opened after 2 minutes, and a focal climbing perch was introduced in to the chamber A and the latency to emerge out to chamber B was recorded.

Experiment III: Aquatic predator

To test the influence of the aquatic predator on the boldness of climbing perch, chamber B of the apparatus was further divided in to two chambers (B and B^1; Fig. 2), using perforated transparent acrylic sheet. A striped murrel (*Channa striatus*; standard length S.L. 20 ± 2 cm, mean ± S.E.) was introduced into chamber B^1. This set-up allows the focal fish in chamber A to see the aquatic predator in chamber B^1, while entering into chamber B. After thirty minutes, the test fish was introduced in chamber A and the latency to visit the chamber B was recorded. A control (II) was also carried out using the same experimental set-up, but in the absence of any predator to check whether alteration in the apparatus had any influence on the boldness of the fish.

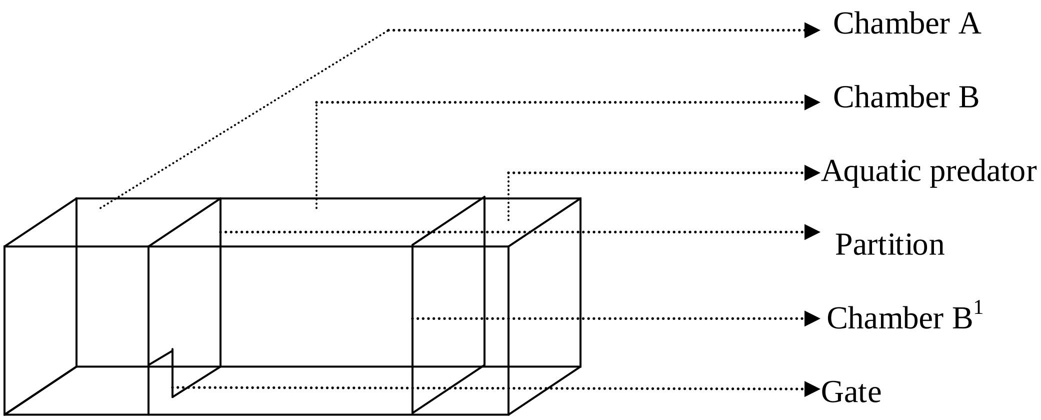


Figure 2. Diagrammatic representation of the apparatus used for testing the influence of aquatic predator on the boldness of climbing perch.

Experiment IV: Alarm pheromone

In order to test the effect of the presence of the conspecific alarm pheromones on the propensity to take a risky decision by climbing perch, the skin extract was prepared by sacrificing 10 donor climbing perch by decapitation with a sharp knife without giving much suffering to the animal (Nordell, 1998). Anaesthetics were not used before sacrificing the fish in order to avoid the possible confounding effect of anaesthetic odour with pheromone (if present) in the subsequent experiments. The skin (which is considered to be a potent source of alarm substances) was removed from each side of the fish and placed in 50 ml of chilled distilled water. Then, it was ground with fine sand and filtered to remove larger particles. The extract was kept in freezer until it is used (Mirza *et al.* 2000; Brown, 2003).

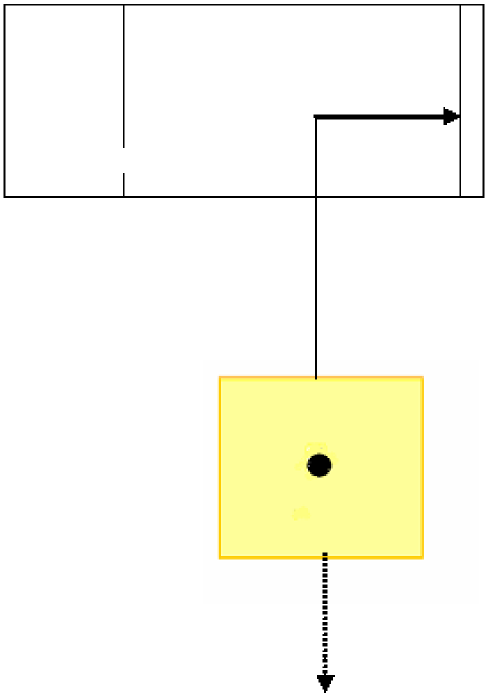
10ml of skin extract was introduced into the water of chamber B and mixed thoroughly using a glass rod. The door on the partition wall was closed while stirring the water, in order to avoid immediate mixing of the alarm chemical with the water in the chamber A. The test fish was introduced into the chamber A, after keeping the door open and the latency to initiate the exploration of chamber B was recorded.

Experiment V: Alarm pheromone and aquatic predator

The potency of alarm pheromones to affect the boldness of the climbing perch in presence of an aquatic predator was also analyzed. Experiment was carried out in the apparatus described in experiment II. After mixing the skin extract (10 ml.) with water in chamber B (as mentioned in the experiment IV) an aquatic predator [striped murrel, 20 ± 2 cm. (SL ± SE)] was introduced in to the chamber B^1. The boldness of the focal fish was measured by introducing it in chamber A. The apparatus was cleaned thoroughly and the stimulus predator was changed after each trial.

Experiment VI: Eye spot

To analyze the influence of the presence of an enlarged eye spot on the boldness of the climbing perch, a yellowish brown coloured screen (32 X 32 cm, Fig. 3) with a shining black spot (diameter 3 cm) in the centre was placed in the chamber B. The test fish was introduced into the chamber A and the latency to initiate the exploration of chamber B was recorded. The boldness of climbing perch in presence of a yellowish brown screen without the black spot (control III) and a black acrylic sheet (control IV) was also tested.



Yellowish brown screen with black spot (3 cm in diameter) in the centre

Figure 3. Diagrammatic representation of the apparatus used for testing the influence of presence of a novel object (eye spot) on the boldness of the climbing perch (Top view).

RESULTS

No significant difference was found in the latency to initiate the exploration of chamber B by control fishes (I, II, III and IV), (Kruskal-Wallis, Test, χ^2 =0.710, N=28; P> 0.05), and most of them entered the chamber B with in 42 seconds (median). This result shows that slight alterations in the apparatus did not cause any marked influence on the boldness of the climbing perch. The present study indicates that the climbing perch exhibited variation in its boldness, when tested in presence of different fear evoking stimuli (Kruskal-Wallis Test, χ^2 =612890, N=28: P<0.001; Figure 4). *Post-hoc* analysis of the data using 'Steel test' (statistical programme KyPlot) has shown that the presence of the predator (both aquatic and aerial), and odour of the aquatic predator failed to affect the boldness of the climbing perch. Additionally, the skin extract of the conspecific alone or in presence of a potent aquatic predator, were found to have no influence on the boldness. However, the presence of a black shining spot on the centre of a yellowish brown screen ('eye spot') significantly reduced the boldness in the fish (Table 1).

	Experiment	t1j	N	P
1	Control X aerial predator	0.1516	28	>0.05
2	Control X aquatic predator	–1.0329		>0.05
3	Control X predator alarm + Aquatic predator	0.29513		>0.05
4	Control X yellowish brown screen without black spot	0.6480		>0.05
5	Control X black acrylic sheet	0.6221		>0.05
5	Control X yellowish brown screen with a black spot	6.1464		<0.001

Table 1. *Post–hoc* (Steel test) analysis of the influence of the presence of different fear evoking stimuli on boldness of climbing perch.

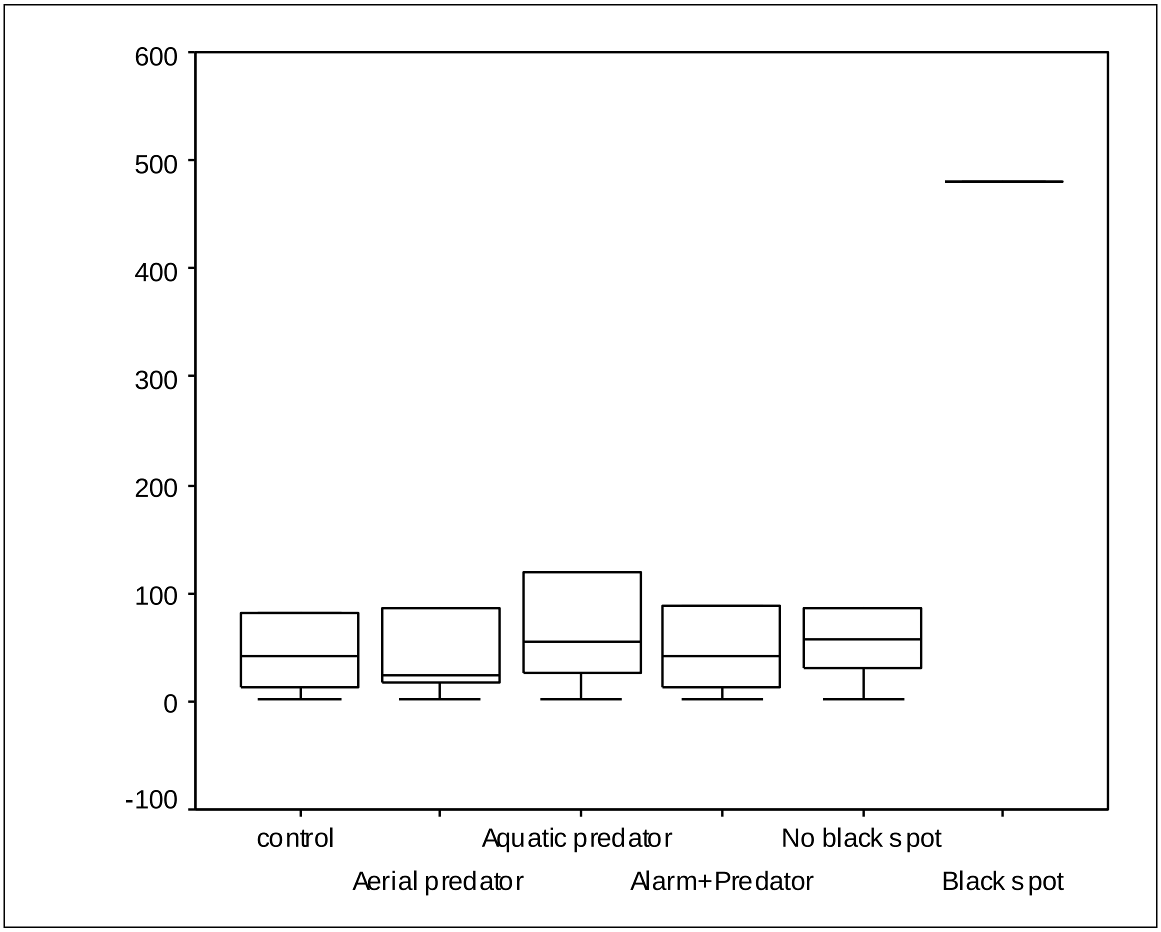


Figure 4. Influence of the presence of different fear evoking stimuli on the boldness of climbing perch (data is represented as median quartile); N=28 for each treatment.

DISCUSSION

It is well established that the presence of predator has a profound influence on the performance of normal behavioural repertoire of the prey fish species (Kelly and Margurran, 2003). In presence of a potent predator, most of the prey species will adopt antipredator strategies like taking refuge or moving away from the place of danger (Dowling and Goding, 2002, Krause *et al.* 1998). Sometimes, the cues announcing the presence of the predator, like the odour, can do the job even in the absence of a live predator (Kelly and Magurran, 2003). For instance, when tested to measure boldness in presence of predator odour, two spotted gobies (*Gobisculus flavescence*) avoided the areas with the odour of the predator cod (*Godus morhua*, Utne-Palm, 2001). However, neither the predator odour nor the presence of predator (no matter whether the predator is aerial or aquatic) was able to influence the climbing perch, while taking a bold decision. The focal climbing perch emerged out of the start chamber in presence as well as in absence of predator/predator odour taking almost the same latency.

The climbing perch did not show any variation in boldness in presence of the skin extract of the conspecifics, which may contain probable alarm pheromones. Even, simultaneous presentation of skin extract with an aquatic predator also failed to initiate fear response in the fish. In contrary to the expected variation in the latency to take a risky decision in the shadow of predator attack, climbing perch never paid any attention to the predator even in presence of conspecifics' skin extract.

All these results converge to the point that climbing perch is a bold fish and the presence of the predator or predator cues have no influence on the tendency of this fish to take risky decisions. The consistency of boldness shown by the climbing perch in situations announcing emergency may be due to the genetically determined and species specific decision making ability. This argument is supported by the findings of Yoshida *et al.* (2005) which demonstrated that the boldness is a species specific characteristic and certain species are bolder compared to other species.

The climbing perch never stopped its exploration just after the entry in to the chamber B; instead, it extended its searching even to the area near the partition wall separating the aquatic predator. Hence, it could be assumed that the climbing perch may have a natural tendency to inspect predators, due to which it neglects the predator or predator cues during the initiation of exploration of chamber B. Kelly and Magurran (2003) reported that on sensing the presence of the predator, many prey fish species increase their search activity to locate it. At the same time, some individuals will even try for the close assessment of the predator to get an overview of its motivational status. Though, a highly adventurous job, the predator inspection behaviour provides the benefits like visual alarm signalling (Murphy and Pitcher, 1987), predator deterrence (Dugatkin and Godin, 1992 a; Godin and Davis, 1995) and bolder males enjoy the preference of females during mate choice situations (Godin and Dugatkin, 1996). Hence, it is possible that climbing perch is a fish showing predator inspection than predator avoidance, as it exhibits exploration of a novel area even in presence of predator or cues associated with the predator.

The introduction of alarm pheromones in presence or absence of the predator is said to have an enhancing effect on the exploratory behaviour of some fish species (Brown, 2003; Kelly and Magurran, 2003). The reason behind this increased interest of the fish to take a risky decision in presence of the predator alarm cues is the reduction of uncertainty of local risk gained, when the position of the predator is located (Kelly and Magurran, 2003). However, in climbing perch there was no variation in the latency to take a bold decision of exploring a novel area, either in presence of conspecifics' skin extract or when the skin extract was presented in combination with the aquatic predator. Hence, these results could be interpreted as, this species possesses an enhanced level of boldness, that it neglects alarm pheromone even in the presence of a predator or the skin cells of the climbing perch does not harbour any alarm substance to initiate fear response.

The consistency of climbing perch in taking a risky decision in presence of biologically significant fear evoking predator stimuli vanished totally, when an eyespot was presented in the novel area. None of the climbing perch tested were bold enough to explore the chamber B, in presence of the eyespot. Therefore, it is assumed that the black spot may resemble the eye of some large organism or it may be acting as a supernormal stimulus for the eye of a predator. This argument is supported the study of Karplus *et al.*(1982), which demonstrated that the shape and size of the eye of aquatic predator have a functional role in the recognition of the predator, when recognition is dependent only upon the frontal view of the approaching predator fish.

According to Rowland (1995), the fishes recognize and respond to two-dimensional and three-dimensional images. However, Bovet and Vauclair (2000) argue that in animals, reaction to pictures is more likely to express confusion between the objects and the picture than discrimination and active correspondence between the two. As far as the exploratory behaviour is concerned, uncertainty of an object present in a novel environment can significantly reduce the exploratory urge of an organism (Berlyne, 1960; Keller, 1987). Thus the climbing perch might have avoided taking a risky decision in presence of the black spot, due to the confusion in the fish evoked by the novel object (Bovet and Vauclair, 2000). The analysis of the motivational basis of boldness using climbing perch as a model system may provide more insight to the risk management strategies of fishes.

Chapter III

Environmental correlates of risky decisions in climbing perch

INTRODUCTION

All animals, including fishes, take adaptive decisions to maximize net energy intake, while simultaneously minimizing the risk of predation (Dill, 1987). However, the nature of the environment (both physical and biological) in which the fish lives, can influence the outcome of any decision (Brown and Braithwaite, 2004a; Brown *et al.* 2007). According Urban (2007), the criterion satisficed while taking a risky decision in one habitat will not provide the same benefit in another habitat with different types of selection pressures. For example, in ecosystems where prey fishes lead an allopatric life with predators, the individuals may hesitate to take risky decisions. While, predator sympatric fishes are more prone to take the risk of exploration of a novel area, because the encounter with a predator is not a rare event in their habitat (Brown and Braithwaite, 2004a). In predator sympatric population the fish can reduce the cost of predator vigilance, if it grows beyond a size, even by taking risky decision to feed in front of a predator (Urban, 2007).

According to Silverman (1978) animals love to explore a novel area because the exploration itself is rewarding. Moreover, the information primacy theory (IPT; Inglis *et al.* 2001) postulates that the animals always patrol their habitat and nearby areas to gather information continuously to deal with the environmental variability. The extension of activities to a new area or the areas with significant difference in properties is correlated with the latent learning, where learning occurs on non-reinforced trials, but remains unused until the reintroduction of a reinforcer provides an incentive for using it (Liberman, 1990). When competition in a safe habitat increases or the benefits from safe habitat decrease, the fish can utilize the knowledge obtained during adventurous exploration and can shift to new areas with more benefit. For example, gold fish is seen to switch patches, when profitability changes (Warburton, 1990).

Like almost all other animals, fishes also extend their activities to the novel areas surrounding their home range (Gerlai and Crusio, 1994). Sometimes, the explorer may perish in predator attack with in a short duration after the entry in to the novel habitat. Hence, Abraham and Dill (1989) predicted that the fish will explore unknown and risky habitat only if it is obligatory. This hypothesis is supported by the observation of Brown *et al.* (2005) which shows that *Brachyraphis episcopi* prefers to spend more time in areas providing more refuge value, even in its famiailr habitat. Additionally, Chapman and Mackay (1984) have demonstrated that the small pikes were not at all interested to leave areas with vegetation cover and spend very little time in open water area of their home range to avoid the risk of aggression from other individuals.

In social fish species, the propensity to take an adventurous decision is not only influenced by the microhabitat conditions but also by the presence of conspecifics (Milinski, 1990a; b). For example, many fish species perform risky jobs like inspecting the motivational status of the predator in pairs to reduce the risk. Sundström *et al.* (2004) point out that the bold individuals are followed by some shy ones to get the benefits of the risk taken by the bold individuals, which may escalate fight and affect the decision to extent the exploration to a new area. Additionally, Jain and Sahai (1989) have demonstrated that several cognitive abilities of the social fish species are affected, when isolated from the group. This chapter describes the influence of the habitat quality and presence of a conspecific on the boldness of climbing perch.

MATERIALS AND METHODS

All fishes were tested in apparatus mentioned in the Chapter1, after making necessary modification, and boldness was quantified following the methodology described in Chapter II. The effect of variation in the habitat quality on the boldness was studied by altering physical or biological properties of the start chamber (chamber A). In all experiments the focal fish was introduced in the chamber A, and the time taken for the initiation of exploration of chamber B was recorded.

Control

In this experiment boldness of the focal fish was measured by introducing it into the chamber A , without making any modification.

Experiment I: Sandy substratum

The bottom of chamber A was covered with washed fine river sand (thickness: 2 cm).

Experiment II: Cobble substratum

The floor of chamber A was covered with a single layer of rock pieces (Cobbles; Size 90 ± 20 mm., Friedman and Sanders, 1978.)

Experiment III: Vegetation cover

The water surface of chamber A was covered with the aquatic plant hydrilla (water thyme; *Hydrilla verticillata*). Here, the bottom of the aquarium (without sand) served as the substratum.

Experiment IV: Vegetation cover and sandy substratum

The substratum of chamber A was covered with sand as described in experiment I and a vegetation cover was provided by spreading *Hydrilla* on the water surface.

Experiment V: Vegetation cover and cobble substratum

Here the rock pieces were spread over the bottom of chamber A and *Hydrilla* cover was provided on the water surface.

Experiment VI: Presence of a conspecific

In order to assess the influence of the presence of a conspecific on the boldness of climbing perch, chamber A of the apparatus was divided into two sub chambers using a transparent Plexiglas (A and A*; Fig. 1). The partition between A and B was replaced with opaque acrylic sheet. In this arrangement the test fish can see the conspecific only when it remains inside chamber A. A conspecific from the home tank of the test fish was introduced in the Chamber A*, ten minutes before the experiment. The test fish was introduced in the chamber A and the boldness was recorded. A control (II) was also carried out using another set of fish in the absence of conspecific, to rule out the influence of the alteration in the spatial properties of chamber A of the apparatus.

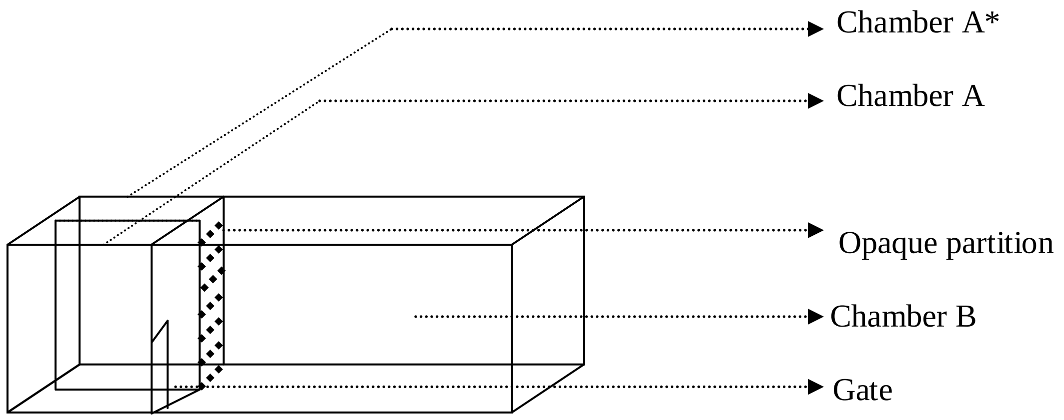


Figure 1. Diagrammatic representation of the apparatus used for testing the influence of the presence conspecific on the boldness of climbing perch.

RESULTS

The results show that alteration in the quality of habitat or the presence of conspecific can influence the boldness of climbing perch (Kruskal- Wallis test, χ^2 =27.462; N=28; P<0.001, Fig. 2).The control fishes reached chamber B with in 42 seconds (median). No significant difference was found in the latency of the initiation of exploration by two control groups (CI and CII; Mann Whitney 'U' test, U=362, N=28; P>0.05). This result indicates that the reduction in the space of chamber A, due to the partition does not influence the ability of this fish to take risky decisions. *Post-hoc* analysis using Steel test (statistical programme KyPlot) shows that sandy substratum, vegetation cover (Steel test, tij=0.492, N=28; P>0.05), and the combination of sandy substratum with vegetation cover failed to influence the boldness of the climbing perch. Meanwhile, a substratum composed of rock pieces (Steel test, tij= -3.485, N=28; P<0.01) or the presence of a conspecific (Steel test, tij= -3.195, N=28, P<0.01) considerably reduced the boldness of climbing perch. When vegetation cover was given in combination with rocky substratum, the fish retained its normal boldness (Steel test, tij = -2.006, N=28; P>0.05).

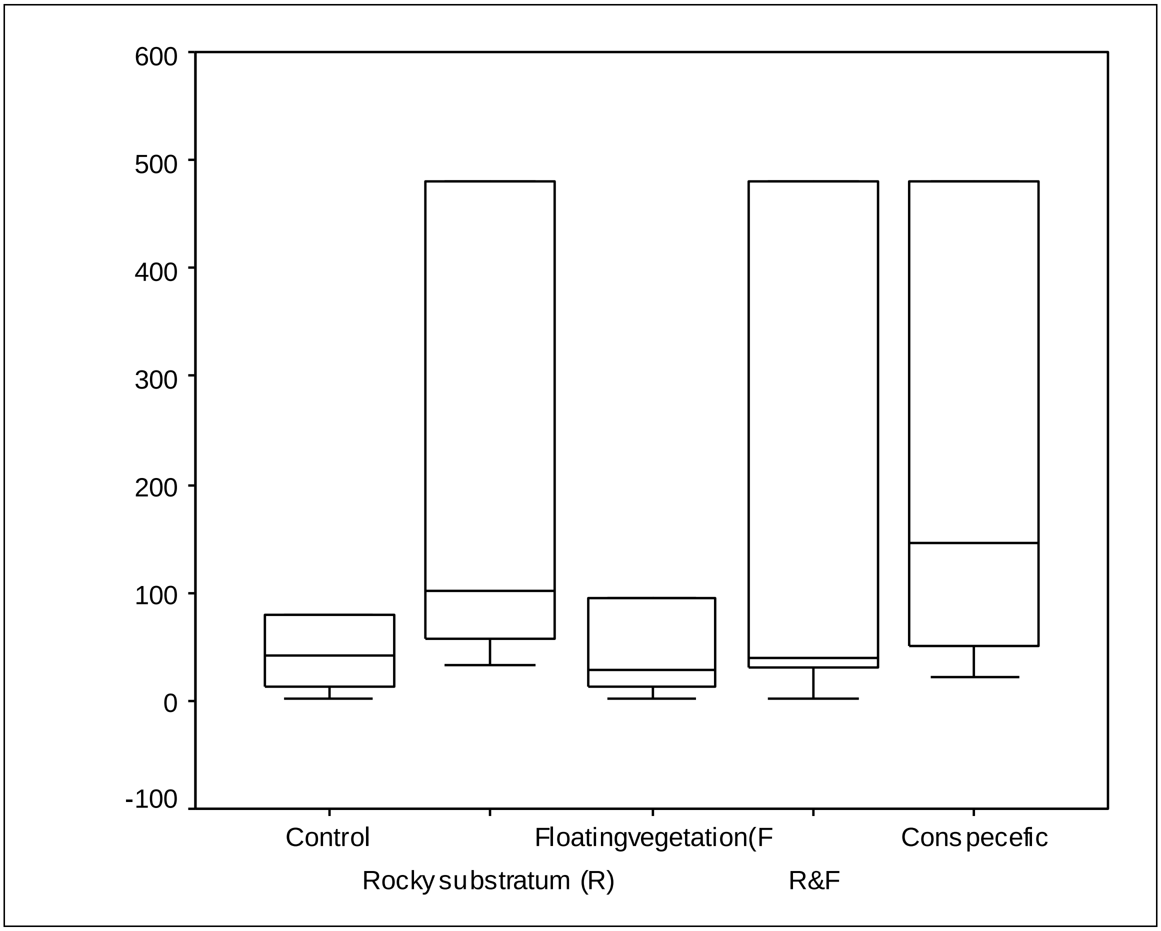


Figure 2. The influence of different environmental conditions and presence of a conspecific on the exploratory behaviour of the climbing perch. Data is represented as median and quartile.

DISCUSSION

The results of the present study demonstrate that the chance of taking a risky decision by a fish is significantly influenced by the properties of the habitat in which the decision is taken. The climbing perch took more time to take a decision of leaving a microhabitat with a substratum composed of rock pieces and to explore a homogenous area without any complexity. The climbing perch restricted most of its activities in the space between the rock pieces and came out of the crevices only for the periodic gulping of the atmospheric air. By contrast, there was no variation in the latency to emerge out from the chamber A from control condition, when chamber A was provided with sandy substratum.

The latency to take a decision of extending activities from a complex microhabitat to a novel homogenous habitat may be an outcome of the variation in the antipredatory strategies utilised by this fish. Hoar and Krause (2003) states that fishes enhance their safety by either joining a shoal or by investing more energy for vigilance. Being isolated from the shoal and provided with a refuge to hide from predator the climbing perch may be utilizing latter strategy, taking refuge than searching for a conspecific or a preferred habitat.

Another hypothesis put forwarded to explain the delay in taking a bold decision in a habitat with substratum made up of rock pieces, is that climbing perch could have a natural preference for a substratum composed of cobbles. Such a natural preference for the substratum of cobbles have been demonstrated in Atlantic salmon, and Kennedy

(1984) advocate practical strategies for the stock enhancement of juvenile Atlantic salmon using stones to satisfy various microhabitat needs.

In the view of Hartzler (1983), substratum with spatial complexity can improve the growth and biomass of the fish by reducing the predation risk, competition and aggression. This hypothesis has been validated using brown trout model system and trout acquired more bio-mass in habitat provided with half-log covers (Hatzler, 1983). So the lack of complexity in the substratum is the suspected reason behind the quick decision to leave the habitat with sandy substratum. Hence, spending more time to take a risky decision to visit an open area, leaving a safe and more beneficial microhabitat with substratum composed of rock pieces, is quite tenable.

According to Killgore *et al.* (1989), the weed cover and bank side vegetation impart determinant effect on the lives of many fish species. The weed cover provides refuge for the prey species and many small sized species restrict their activities under the cover vegetation and always avoid the open areas of the water body to reduce the predation, inter and intra-specific aggression (Durocher, *et al.* 1984; Chapman and Mackay, 1984; Grimm, 1981 a;b). Though, the substratum composed of cobbles increased latency of taking a risky decision, the vegetation cover was unable to impart any influence on the boldness of the climbing perch. Moreover, the reduction of boldness induced by the substratum composed of cobbles was abolished and the climbing perch left that area, when a vegetation cover was given in combination.

Thess results can be explained by the following hypothesis: the presence of a vegetation cover increases the refuge value of chamber A (Brown *et al.* 2005) and climbing perch can boldly extend its activities to an open area, because it can quickly retreat to the safety of vegetation cover, in case an aerial attack. Hence, it could be assumed that presence of a vegetation cover near the open area might be improving the boldness of climbing perch that it moves from beneficial microhabitat with substratum composed of rock pieces to risky open area.

In presence of a conspecific, the climbing perch reduced its boldness and spent more time in the shelter chamber. Here, instead of exploring a novel area, the fish always tried to join the conspecific present in the nearby chamber. The reduction in the tendency to explore a novel area in presence of conspecific may be the result of shoal living nature of this species. Many studies show that shoaling fish give more importance to the conspecific (Hoare and Krause, 2003). Climbing perch may also be giving more importance to stay with conspecifics than obtaining benefits from exploring a novel area.

It could be concluded that in climbing perch, the nature of microhabitat in which the decision is taken as well as the presence of a conspecific can influence the boldness. This result is supported by the finding of Coleman and Wilson (1994), which states that the propensity to take a risky decision is a context specific behaviour and the fish may exhibit variation in the boldness according to the characteristics of microhabitat in which the risk is taken. In addition to the habitat quality, the sociobiologically important factor conspecific is also found to be influencing the boldness of the climbing perch. Hence, the studies dealing with the genetical and environmental correlates of propensity to take a risky decision can throw more light on the biological basis of the boldness and its influence on decision making ability of fishes.

Chapter IV

Development of boldness

INTRODUCTION

Environmental conditions experienced during the early phases of life are crucial for the normal development of vital behaviour patterns of an animal (Futyama, 1998; Salonen, 2005). This is also true in the case of the trait boldness-shyness continuum.The determinant effect of early experiences on boldness of a fish is demonstrated by Tully and Huntingford (1987) using sticklebacks. These authors demonstrated that the boldness of this fish is affected by the level of chasing by fathers during early life. A recent study using the species *Brachyraphis episcopi* also supports this finding (Brown *et al.* 2007). Here, the first generation larvae reared in a homogenous laboratory condition, but experienced repeated chasing using a net, exhibited increased level of boldness. Additionally, Salonen (2005) points that the fish larvae developed in the hatchery conditions, with reduced environmental complexity, exhibited variation in boldness compared to their conspecifics living in the natural water bodies.

According Braithwaite and Salvaness (2005) safety and homogeneity provided by the hatchery conditions are the basic causative factor for the abnormal development of boldness in hatchery reared fish. Thus, the lack of variation in the stimuli to elicit diversity in the behavioural profile and the reduced need of behavioural flexibility in the due course of early life in a homogenous condition could create an adult fish with reduced cognitive ability and malformed behavioural and neural plasticity (Hunter *et al.*

2002; Kempermann *et al.* 2002; Grand and Grant, 1994). The major ecological parameters that have most often suggested to affect the development of risk taking ability of a fish are high rearing density (Cabellero and Castro-Hdez, 2003; Sundström *et al.* 2004), feeding in excess at a predictable place (Grand and Guha, 1993), and the lack of presence of predators (Braithwaite and Salvaness, 2005).

There are studies showing that simple exposure to varying spatial and foraging cues during the early days of life can help the fish larvae and check the malformed development of boldness. For example, cod (*Godus morhua*) larvae developed in a plain hatchery tank were with very poor boldness, while larvae experienced spatial heterogeneity either on its own or in combination with varying food availability in the hatchery tanks were quick in taking risky decisions like leaving the enclosed start box to explore a novel area (Braithwaite and Salvanes, 2005).

In natural water bodies, juvenile fishes will have to face many situations where bold decisions are to be taken (Brown *et al.* 2007). They have to learn new routes to the feeding grounds and shelters for escaping from predators (Sundström *et al.* 2004). Young inexperienced fishes develop a menu from the food materials available in its home water by exploring novel objects. Many of these explorations are carried out under the threat of predation (Magnhagen, 2006). According to Brown (2003) many antipredator tactics are learned either from a real situation or from conspecifics through social learning.

If the larvae develop in a homogenous condition, the chances to get experience with different environmental factors are scanty and the conspecifics are also ignorant of predators and novel food items, the chance of any sort of social learning is denied. For example, when the food is assured and provided *ad lib.* at a particular place during younger days of development, the fishes will not be able to develop a menu (due to the poorly developed exploratory behaviour) and will consume even non palatable materials resembling food materials present in its vicinity (Brown and Day, 2002). Additionally, these inexperienced fishes will exhibit poorly developed antipredatory tactics and will take lethal decisions like exploring a hungry predator due to the underdeveloped predator inspection ability. Moreover, these fishes will not be able withstand a real predator attack, because, to escape from a predator requires more than just an ability to recognize the threat (Braithwaite and Salvanes, 2005). Hence, fish bred in such undiversified habitat for several generations will become bolder due to the relaxed selection pressure on antipredator behaviour (Fleming and Einum, 1997).

According to Salonen and Peuhkuri (2004), the alteration of boldness does not require the selection for many generations in a less complex habitat. In a study using European graylings (*Thymallus thymallus*) these authors have demonstrated that only one generation in a homogenous habitat can increase the time required for taking a risky decision by a species. However, European greylings originated from the same hatchery stock, in two different years and undergone the same course of experience in a habitat without any complexity, showed variation in boldness (Salonen, 2005). The present chapter gives an account of the development of boldness in two groups of climbing perch kept in homogenous condition for two different durations. Additionally, the boldness of these two groups of fishes was compared with the conspecifics of similar age collected from the natural water bodies.

MATERIALS AND METHODS

Collection and maintenance of breeders

Breeders were collected from ponds of Irinjalakuda, Thrissur District, Kerala State, India and maintained in circular cement tanks, out side the laboratory. Each tank was with a dimension of 3 m diameter and a depth of 2 m. Jumping out of fishes was prevented by covering the mouth of the tanks with iron grids. A shade was provided using cotton cloth to reduce the excessive sunlight and temperature fluctuation in the water column. Water level was maintained at the height of 1.7 m. Fifty fishes were stocked in each tank without segregating the sex. Artificial food pellets (Higashimaru, Japan) was given *ad lib*. twice daily (morning and evening). The water was changed once in a month. All fishes were stocked during the period of April–May.

Induced breeding

In order to acclimatize the fishes with the laboratory conditions, healthy females (gravid) and males were selected and transferred to glass aquarium (80 x 40 x 60 cm) seven days before subjecting them for induced breeding. In this species, males are smaller in size compared to the females and the former had a slender body form in comparison to the latter. The gravid females of size 7 ± 2 (standard length S.L. ± S.E.) and the males having the size 4 ± 0.5 cm (S.L ± S.E.) were sorted for breeding. The sexual maturity of the males was confirmed by stripping and only the males with the presence of milt were used. A pair of males and a female was kept in an aquarium (50 x 40 x 30 cm) covered with a steel grid, one day before the administration of artificial hormone. The water level was maintained at a level of 40 cm. The fishes were induced to breed only after the onset of monsoon (after June 15), a season when most of the fish species inhabiting the freshwaters of Kerala breed.

The males and females were administered with artificial Gonadotropine releasing hormone (GnRH; OVAPRIM; Syndal Lab, Vancoure, Canada) on the caudal peduncle. The dosage of this intramuscular injection was 0.5 ml/kg body weight of the fish. The injected breeders were transferred back to their home aquaria and simulated rain was given using a sprinkler. The aquarium was covered using the steel grid and fishes were kept in an ambience without much disturbance. The hormone injection was given in the evening (after 5.00 p.m).

Collection of eggs

The spawned male and female were removed from the breeding tank on the next morning of hormone injection. Eggs were collected from breeding aquarium by siphoning water to a net using a rubber hose. The unfertilized eggs (milky white in colour) were removed. The healthy eggs (transparent in nature) were separated from the debris and transferred 15 eggs each to 500 ml beakers filled with filtered pond water. The filtering of the pond water was carried out to remove the zooplankton which may destroy the eggs or hatched out larvae. All beakers were covered with fine mosquito net to avoid the consumption of the larvae by aquatic insects. Water level was maintained at a height of 8cm. Up to 48 hours after the fertilization, 98 ± 3% of eggs were hatched out in to the larvae. The dead eggs, chorion, and the larvae with morphological deformities were removed.

Maintenance of larvae

The number of larvae was maintained to 15 in all beakers by adding larvae (in case of death) from other beakers. However, no larvae were added or removed after fifth day of hatching to avoid any confounding affect on the normal development of their social cognitive abilities. The sides and bottom of the larval rearing beakers were covered using white paper to avoid the interference of any external cues and to simulate a homogenous atmosphere present in the hatchery conditions.

The larvae were fed with artemia nuplii for 14 days, after the complete absorption of yolk (4th day after hatching). From 14th day onwards artificial larval food Piscimix was given in combination with artemia nuplii. As the larvae grown in size, the menu was shifted to food pellets (Higashimaru, Japan).

One month old juveniles were transferred from the beaker to white fibre tubs (45 x 30 x 30cm) covered with steel grids. The fibre tubs provided the larvae more space for locomtion and a homogenous environment without any spatial or structural complexity, a condition similar to the hatchery. Only the beakers containing 14 to 15 juveniles were emptied to the tubs. Food pellets were given *ad lib.* twice daily morning and evening. Water was changed with in an interval of seven days. These juvenile fishes were allowed to grow in the same tub up to the date of experiment. Only the fishes from the tubs with at least 13 members were used for the experiment.

Controls

Climbing perches were collected from nearby ponds and fishes of age 0+ and 1+ were segregated. The age of the fish was determined by counting the growth rings on the scale (Lagler *et al.* 1962; Tandon and Johal, 1996). Only fishes, with a size similar to that of six month old fishes grown in artificial cement tanks maintained like natural ponds, were sorted to use as control I. These fishes were with a size of 5. 2 ± 1.3 cm (S.L.±S.E.) and were olive green in colour with dark stripes on the body. They were with a prominent dark spot on the caudal peduncle.

Fishes of the age 1+ (size 7.6 ± 1cm; S.L.±S.E.) were used as control II. These fishes were also dark olive green in colour, but the black stripes on the body and the spot on caudal peduncle were faded in nature.

Focal fishes (reared in the laboratory)

1. six month old fish

These fishes were pinkish white in colour and were very small in size (3.4 ± 0.5cm; S.L. ± S.E.; N=50) compared to the fishes of the same age, colleted from the natural ponds. The stripes on the body of these fishes were not dark and clear.

2. 14 month old fish

These fishes were small in size (4.5 ± 0.5cm S.L.±S.E; N=50) and whitish in colour compared to their conspecifics collected from the natural habitats.

Testing of boldness

Swim-way apparatus

An aquarium of size 60 x 32 x 32 cm was converted in to the swim-way apparatus by dividing it in to two chambers [Chamber A (20 x 32 x 32 cm) and Chamber B (40 x 32 x 32 cm)]. The partition was an opaque Plexiglas sheet with a gate (8 x 4 cm) on a corner. The chamber A was made opaque using black acrylic sheets. Three sides of the aquarium were covered using black paper to avoid any sort of external interference. Here, the small chamber (chamber A) functioned as the start chamber and chamber B was the swim-way. The ceiling of the start chamber was covered using an opaque acrylic sheet to provide the necessary shade for the fish staying in chamber A. This apparatus was illuminated by a compact florescent lamp (20 W) suspended on the top of the assembly. Differing from the apparatus used in other experiments, the swim way apparatus was used in all experiments described in this chapter only, because the ambience available in the home tanks of the fishes born and brought up in the laboratory had many similarities with the apparatus used in the earlier experiment. Hence, the confounding effect of the difference in experience with the habitat on the boldness can be avoided, if swim-way apparatus is used for the quantification of boldness, as the fish collected from the field and fish reared in the laboratory were unfamiliar with such an environment.

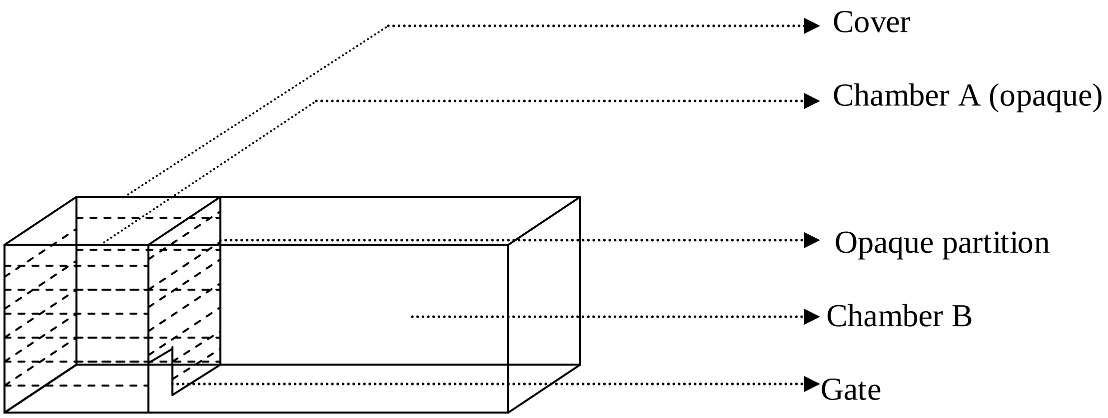


Figure 1. Diagrammatic representation of the swim way apparatus used for testing the boldness of climbing perch.

All fishes used in this experiment were given experience of five minutes, with the experimental arena for four days consecutively. After coming out of the chamber A, the focal climbing perch was given five minutes for the exploration of chamber B. On the fifth day, individual focal fish was introduced into the chamber A and the latency to initiate the exploration of chamber B was recorded. The initiation of exploration is defined as the time taken by the fish to come out of the chamber A through the gate provided. If any fish fail to come out from chamber A after 6 minutes the trial was terminated and the fish was allocated a ceiling value of 360 seconds. 28 individual climbing perch were tested from each group. After the experiment, all fish collected from the natural water bodies were released back into the site of collection and the lab reared fishes joined the induced the breeding programme conducted by Animal Behaviour and Wetland Research Laboratory, Christ College.

RESULTS AND DISCUSSION

According to Brown and Day (2002), development of fish larvae in undiversified atmosphere can lead to the malformation of decision making ability. For example, the brown trout developed in a homogenous condition were bolder in nature (Sundström *et al.* 2004), while European graylings experienced a similar condition exhibited a reduced level of boldness (Salonen, 2005), compared to their conspecifics living in a heterogeneous environment. Moreover Álvarez and Nicieza (2003) using brown trout model system have demonstrated that one generation in a homogenous habitat can generate divergence in the the ability to make risky decisions. In contrary, the first generation climbing perch born and brought up in a consistent condition for a duration of 14 months failed to exhibit any significant variation in their propensity to take a risky decision compared to their counter parts collected from the natural habitat (Kruskal Wallis test; N=20; P> 0.05; Fig. 2) The laboratory reared fishes came out of the opaque start chamber quickly and started the exploration as done by the fishes collected from the wild habitat.

This, result leads to a hypothesis that, in climbing perch, boldness have a genetical background and this inherited boldness may not vary up to one generation even in a homogenous condition. A similar result was obtained by Brown *et al.* (2007) in a poecilid fish *Brachyraphis episcopi*, where, the first generation fishes developed in a homogenous atmosphere took a risky decision of entering a novel habitat from a shelter chamber with a latency equivalent to the wild fish. The genetical background of boldness is also proven by Iguchi *et al.* (2001) using two strains of cloned red-spotted cherry salmon, *Oncorhynchus masou macrostomus*, and by Vilhunen *et al.* (2008) using brown trout model system.

Though, there are evidence supporting genetic control of boldness, Braithwaite and Salvanes (2005) argue that living for a long time in a homogenous condition can affect the development of boldness in a fish. Their study using cod larvae shows that exposure for 14 weeks in a homogenous condition increased the tendency of the larvae to initiate exploration of a novel area. The elevated levels of boldness reduced subsequently as the time spend in the homogenous condition increased. However, living for six months in a homogenous condition in the laboratory did not affect the boldness of climbing perch. This fish exhibited a similar propensity to take a risky decision as the six month old juveniles from the wild habitat. Additionally, the comparison of the latency to take a risky decision by the climbing perch of age six months and fourteen months also failed to show any significant difference. This result suggests that genetic factors have a dominant role over environmental factor on the development of boldness of the first generation young ones of climbing perch.

The climbing perch born and brought up in the hatchery conditions were very small in size compared to the individuals of the same age inhabiting natural water bodies (ANOVA $F_{3,199} = 23.510$; $P<0.001$, Fig. 2). According to Ryer and Olla (1997), the fishes developed in heterogeneous condition spend much of their energy in tasks other than feeding, with the cost of lower growth rate. This result is supported by the study of Braithwaite and Salvanes (2005) using cod (*Godus morhua*). However, climbing perches developed in homogenous condition with food *ad lib.* exhibited a reduced growth rate. The reason behind the reduced growth rate of climbing perch developed in artificial homogenous habitat with food *ad lib.* offers a new area for future research .

The variation in the size of climbing perch developed in the lab and field conditions become significant, when compared with studies of Brown *et al.* (2005; 2007) in *Brachyraphis episcopi*. These authors have demonstrated that larger fish always spend more time in side the shelter chamber before taking a risky decision compared to the smaller fish, indicating a correlation of boldness with the body size. By contrast, in climbing perch the trait boldness was found to be independent of the body size. Here, six month old fishes reared in the laboratory condition as well as 1+ climbing perch from the wild habitat exhibited almost similar boldness, though there was a pronounced variation in their body size. This results also indicate that the application of metabolic hypothesis of boldness (stating that the higher metabolic rates of young fishes will compel them to take risky decisions quickly in order to compensate the high energy demand) is not possible in the case of climbing perch.The results of the present support the observations of Sundström *et al.* (2004) which deny any correlation between metabolic rate and boldness.

Brown *et al.* (2004) suggest that experience with predator can reduce shyness, and the individual fishes leading a predator sympatric life are more prone to take risky decisions. Contrary to the above hypothesis, Brown and Laland (2001) state that predator naive fishes from homogenous atmosphere will be more interested in taking risky decisions due to the unawareness about the danger. However, comparison of the boldness of climbing perch reared in the laboratory (in absence of any predator cues) with members of natural population living under high levels of selection pressures, like spatial complexity and unpredictable food availability, and predators failed to show any significant variation. Hence, the scientific basis of the consistent boldness in climbing perch is to be analyzed in detail. Moreover, future studies analyzing the development of boldness in climbing perch will help us to understand the scientific basis of development of boldness in fishes.

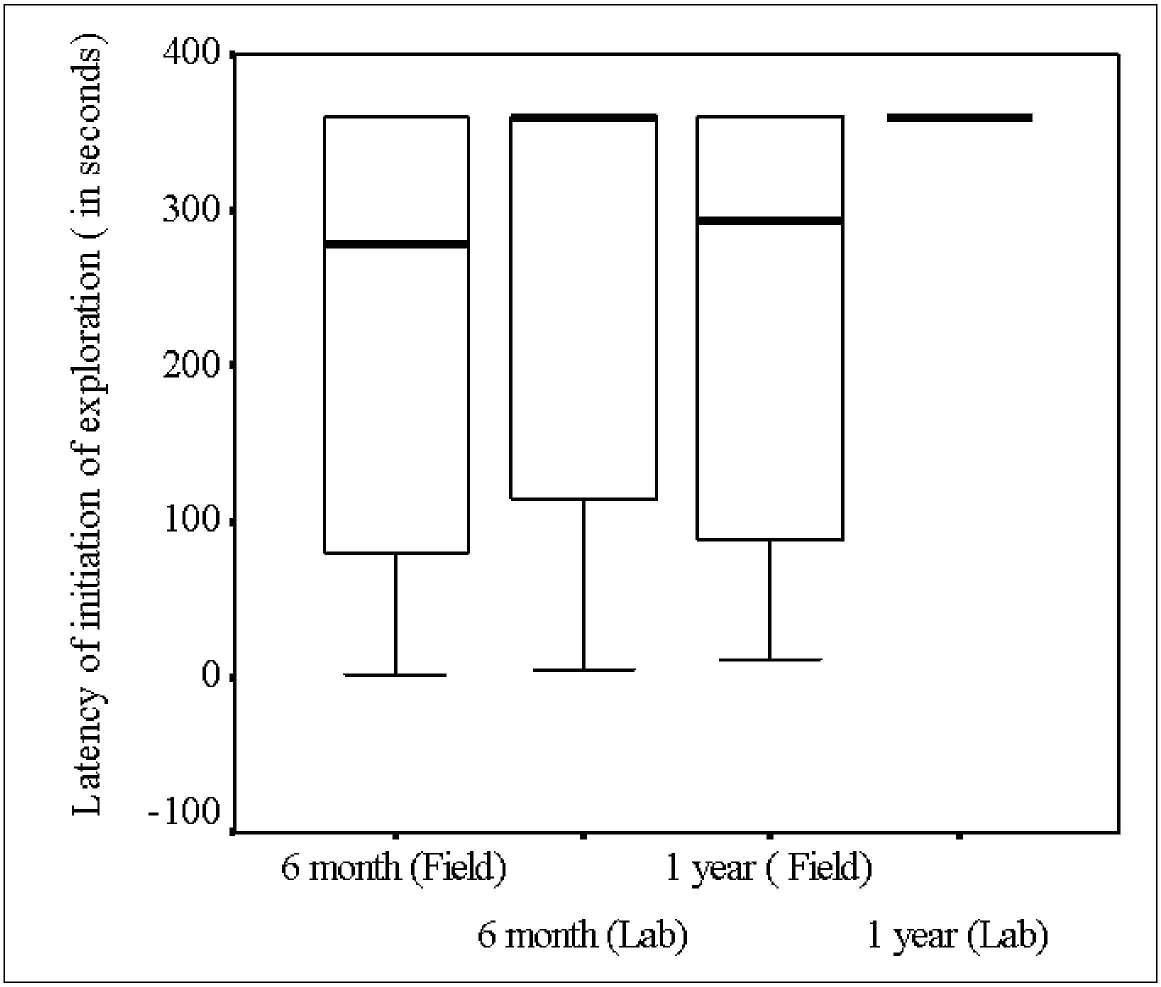


Figure 2. Comparison of development of boldness of climbing perch reared in a homogenous habitat and collected from natural habitat.

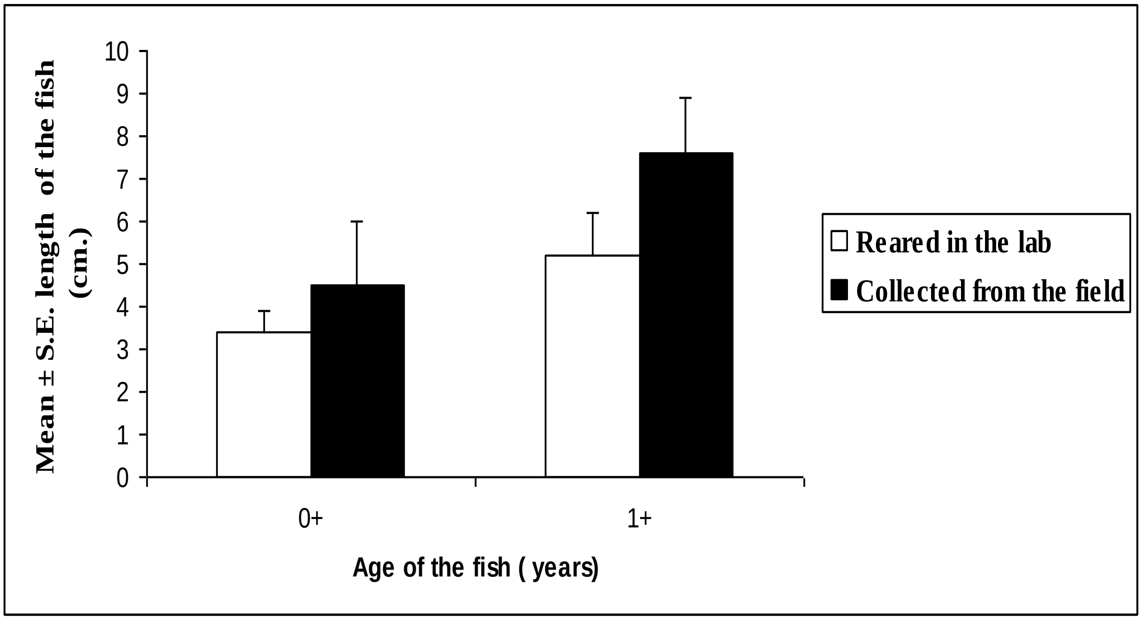


Figure 3. Influence of the rearing conditions on the growth of climbing perch

Section summary

Boldness: the propensity to take a risky decision

The climbing perch was found to a bold fish; dare to take risky decisions in most of the experimental situations. Their shyness : the latency to initiate the exploration of a novel habitat, reduced with the increase in the familiarity with the environment after repeated exposure. Moreover, these fishes will attain steady level of boldness by the fourth day of repeated exposure. Furthermore this level of boldness was almost consistant in various occasions. For example, the presence of fear evoking cues like predator (both aquatic and aerial), skin extract of the conspecific (probable source of alarm pheromone), and the combination of predator with predator alarm cues failed to affect the boldness of this fish. In contrast, the presence of a novel object simulating an eyespot was found to be potent to inhibit the fish from taking a risky decision of exploring a novel area.

The nature of the habitat in which the fish makes a decision also can affect its boldness. The climbing perch retained their natural boldness in habitats with covering vegetation and sandy substratum. The combination of sandy substratum with vegetation cover also failed to affect the boldness of the fish. However, in a habitat with substratum made of cobbles, this fish preferred to stay inside the crevices present between the cobbles and avoided taking any risky decisions. This reduced boldness in a habitat with a substratum composed of cobbles retained its normal value, when a vegetation cover was given in combination with it.

The climbing perch born and brought up in the homogenous habitats for one year exhibited similar degree of boldness shown by the fishes of same age collected from the wild habitats. These results point to the assumption that, in this species boldness is a genetically determined trait.

CONSOLIDATED DISCUSSION AND CONCLUSION

Owing to the repeated findings discussed in this thesis, it could be suggested that climbing perch can assess and attribute values to different stimuli perceived, and can make decisions based on the expected benefit (Binoy and Thomas, 2004; 2006). This fish was found to be an excellent decision maker in two major contexts of decision making analysed: the shoal selection a (binary choice situation) and exploration of a novel area (taking a risky decision).

When presented with a combination of familiar and unfamiliar shoals with variation in size, the climbing perch decided to join with the larger shoal, a decision reported in many fish species (Morrel *et al.* 2007). This result reveales a determinant role of shoal size and the the benefit obtained by the fish in joining a large group, on the shoaling decision of this species. Though, preference for larger shoal over smaller one is an instinctive behaviour, the factor familiarity was found to be strong enough to influence the decision making ability of this species. The climbing perch was able to distinguish familiar individuals from unfamiliar ones, as well as familiar shoal from unfamiliar shoal (Binoy and Thomas, 2004; 2006). Moreover, they preferred to join with the familiar individual or the shoal, over unfamiliar individual or shoal. However, the full-fledged effect of familiarity on the decision making was expressed only when the size of familiar shoal was equal to that of unfamiliar shoal. In all other situations, the decision was biased towards the larger shoal and trading off point between familiarity and shoal size was 1:1.9 (familiar shoal: unfamiliar shoal).

In climbing perch, the shoaling decisions were always biased towards conspecifics; but experience for a longer duration with heterospecific can bring on familiarity with it, and the familiarity thus formed can influence the shoaling decision. Interestingly, only the heterospecifics, having a shape similar that of conspecific was able affect the decision making ability on the basis of acquaired familiarity. However, the heterospecific with a body shape different from that of conspecifics failed to induce familiarity in climbing perch, as well as to influence their shoaling decision. Hence, it could be suggested that the experience for a long period can induce familiarity based decision bias in this species, if the other factors (for example, shape of the heterospecific) favour the familiarity acquisition mechanism.

Familiarity can affect the propensity to take a risky decision (boldness) by climbing perch, a phenomenon reported in many other fish species (Iguchi, 2001; Yoshida *et al.*, 2005; Vilhunen *et al.*, 2008). The latency to take a risky decision reduced significantly when the fish became familiar with the situation.

The boldness in this species seems to be a genetically determined trait. The basis of such a hypothesisis is that, this fish exhibited a consistant level of boldness in different contexts and even in presence of biologically significant fear evoking stimulus like predator. Moreover, development in a homogenous environment without having any experience with external cues for one year failed to influence the propensity to take a risky decision, supporting the genetic determination of boldness in this species.

However, some external factors were found to influence the descision making ability of this species. For example, a novel object simulating an eyespot, as well as microhabitat with substratum made of cobbles were able to inhibit climbing perch from taking a risky decision. These results show that, though the boldness is consistent in climbing perch, this fish makes decisions flexibly in accordance with the demand of the situation.

In climbing perch, many of the decisions are influenced by visual cues rather than olfactory cues. The presence of olfactory cues like odour of conspecifics, skin extract of conspecifics (probable source of alarm pheromone), and the mucous secretion of predator were ineffective to impart any influence in different decision making situations analysed. However, an eyespot and heterospecific having a shape similar to that of conspecific (visual cues), were able to affect the decision making ability in this fish. Therefore it could be assumed that this fish is highly depended upon visual cues for gathering information. Hence, climbing perch provides an excellent model system for studying the cognitive abilities of fishes.

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List of Publication

In Journals

1. **Binoy V.V. and John Thomas K**. (2008) Influence of hunger on the food stocking behavior of climbing perch. ***Journal of Fish Biology*, 73: 1053-1057.**
2. **Binoy V.V. and John Thomas K**. (2006) Climbing perch (*Anabas testudineus)* can recognize members of a familiar shoal. ***Current Science*, 90 : 288-289.**

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3. **Binoy V.V. and K. John Thomas** (2004) The Climbing perch (*Anabas testudineus*- Bloch), a freshwater fish, prefers larger unfamiliar shoals to smaller familiar shoals. ***Current Science.* 86 :** 207-211.

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4. **Binoy V.V. and John Thomas K.** (2005) Comparative analysis of organochloride and organophosphate pesticides on the learning ability and sustained swimming capacity of a fresh water fish. ***Journal of the Indian Society of Toxicology,* 2: 23.**
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1. **Binoy, V.V., Adhem Shahin and John Thomas K.** (2007) Bio- film formation in *Euglena gracilis:* the influence of time of the day and wavelength of light. National symposium of chronobiology 2008, Madurai Kamaraj University, Madurai.
2. **Binoy V.V. and John Thomas K.** (2007) **T**he influence of hunger on food stocking behaviour of climbing perch, a freshwater fish. Abstracts of the 31st Annual conference of the Ethological Society of India. pp. 110
3. **Avinash ,T.A. Binoy V.V. and John Thomas K.** (2007) Analysis of route learning ability of climbing perch, Abstracts of the 31st Annual conference of the Ethological Society of India. pp. 108.

4 . **Shiron, J., Binoy V.V. and John Thomas K.** (2007) Predator avoidance behavior of naïve juveniles of *Puntius sarana* a fresh water fish. Abstracts of the 31st Annual conference of the Ethological Society of India. pp. 109.

4. **Binoy V.V. and John Thomas K.** (2005) Individual recognition in a fish, the climbing perch, (*Anabas testudineus)* and the cues involved in the formation of familiarity. Abstracts of the 29th conference of Ethological Society of India p 51.

6. **Binoy V.V. Sandhya V.V. and John Thomas K**. (2005) Altered environment alters stimulus–response paradigm: Effect of pH and salinity on the ontogeny of behaviour in *Heteropneustes fossilis*, A freshwater fish. Abstracts of the 29th conference of Ethological Society of India.. p. 52.

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