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Fish cognition: a primate's eye view

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Abstract We provide selected examples from the fish literature of phenomena found in fish that are currently being examined in discussions of cognitive abilities and evolution of neocortex size in primates. In the context of social intelligence, we looked at living in individualised groups and corresponding social strategies, social learning and tradition, and co-operative hunting. Regarding environmental intelligence, we searched for examples concerning special foraging skills, tool use, cognitive maps, memory, anti-predator behaviour, and the manipulation of the environment. Most phenomena of interest for primatologists are found in fish as well. We therefore conclude that more detailed studies on decision rules and mechanisms are necessary to test for differences between the cognitive abilities of primates and other taxa. Cognitive research can benefit from future fish studies in three ways: first, as fish are highly variable in their ecology, they can be used to determine the specific ecological factors that select for the evolution of specific cognitive abilities. Second, for the same reason they can be used to investigate the link between cognitive abilities and the enlargement of specific brain areas. Third, decision rules used by fish could be used as 'null-hypotheses' for primatologists looking at how monkeys might make their decisions. Finally, we propose a variety of fish species that we think are most promising as study objects.

Keywords Fish · Primates · Cognition · Intelligence · Learning

Introduction

Recently increased interest in cognitive aspects of the behaviour of animals is connected with advances in the development of both theoretical frameworks and methodology. Cognitive psychologists have adopted a more evolutionary approach to cognitive research (see historical review in Kamil 1998). The major contribution of primatology to cognitive psychology was arguably the development of the social intelligence hypothesis (Humphrey 1976; Byrne and Whiten 1988; Dunbar 1992), which states that the evolution of cognitive skills together with a large neocortex in primates was caused by the social complexity typically found in primate groups. This idea challenged the widely established view that primates need their intelligence to cope with the demands of a complex diet (e.g. Clutton-Brock and Harvey 1980). Regarding methodology, Heyes (1993, 1994) pointed out that many purported cognitive skills of primates like imitation learning or theory of mind had never been shown properly, that is, with a rigorous experimental design that could exclude simpler mechanisms.

Two approaches are currently used to examine cognitive questions. First, comparative analyses on the level of species correlate the size of specific brain areas like the neocortex with measures of social complexity or measures of diet complexity (Dunbar 1992; Barton 1995, following Jerison 1985). Second, scientists test and document cognitive skills in their study animals, sometimes testing several species with the same experimental design (e.g. Visalberghi et al. 1995; Tomasello et al. 1998). A meta-analysis will eventually reveal whether there is a stepwise decrease from humans to apes to monkeys to prosimians in the number of skills found in each of these groups. Still, it should be clear that any skills that might be found in humans and apes are merely candidates for complex cognitive skills. Ultimately, the involvement of the neocortex in producing the skill has to be evaluated.

Studying cognition in primates with a comparative approach is certainly of particular value for increasing our understanding of human intelligence and brain size. Still, the comparative approach is also very useful for comparing more diverse taxa with each other, for example, the various mammalian orders, or mammals with birds, reptiles, amphibians, and fish (Kamil 1998). First, a comparison might reveal whether there are cognitive problems typically faced by primates but rarely by other taxa. Such cases would be promising candidates for the emergence of cognitive skills, which promoted the enlargement of the neocortex in primates. Second, one could correlate various skills with brain (area) sizes in a variety of taxa to see whether a general pattern emerges, for example, whether social competence is always correlated with neocortex or homologous brain area enlargement, not only in primates but also in other mammals, birds, or fish.

Unfortunately, few scientists outside primatology realised that the advances in theory and methodology could be used for research in other taxa as well, a positive exception being cognition in birds (Marler 1996; Balda et al. 1998). This is unfortunate as it is increasingly acknowledged that ultimately, the mechanistic approach to cognitive research should be embedded in the evolutionary history of species (Dunbar 1992; Barton and Dunbar 1997; Tomasello and Call 1997; Balda et al. 1998). As in other fields of animal behaviour, the general expectation should be that similar ecological (social or environmental) pressures will lead to similar adaptations in a variety of species, even those of different taxa (see Wilson 1973). It would be important to know whether different taxa have to use the same cognitive mechanisms for similar problems, or whether a variety of simple and more complex mechanisms can achieve the same goal. In the latter case, further research should focus on asking whether the complex (and probably expensive in terms of brain size) mechanisms yield any advantage over simple (and probably cheap) mechanisms.

In this article, we provide selected examples from the literature on cognitive aspects of fish behaviour and compare the evidence to what is known about primates, but we largely ignore other taxa. Our approach is thus very similar to that of Marler (1996), who compared the knowledge on social cognitive abilities of birds and primates. Fish were almost completely excluded from the new wave of cognitive research and play a minor role in recent textbooks on cognition (but see Shettleworth 1998). There are some good reasons for this. A major part of the fish literature is rather descriptive and/or deals with functional rather than mechanistic aspects of behaviour. This means that in our article, we rather have to restrict ourselves to describing the phenomena, such as co-operative hunting, cheating, reconciliation, and so forth, that are found in fish in a functional way, without insisting that the underlying cognitive processes be shown according to modern standards. When we say, for example, that a cleaner fish cheats its client, all we know is that the cleaner fish performs an act, which increases its own fitness at the expense of the client's fitness, that is purely functional. We do not imply that the existence of such a phenomenon can tell us anything about what happens in the cleaner's brain shortly before or during the event. Still, we think that on this descriptive functional level, we are able to provide fish examples for almost all phenomena that are currently being discussed in the context of primate intelligence. We also recommend looking at the many examples of fish behaviour provided by Helfman et al. (1997), which could be studied from a cognitive perspective. We will therefore argue that listing what primates can do will not suffice to separate them from other taxa. Instead, comparative studies on the exact underlying mechanisms and decision rules, and the quantification of abilities might reveal the important differences.

Since the Machiavellian intelligence hypothesis distinguishes between social intelligence and environmental intelligence (Byrne and Whiten 1988), we tried to structure our examples according to these two categories. Still, it should be clear that these categories are at least sometimes linked, as social learning can be used as a mechanism to acquire knowledge about both other group members (e.g. learning rank order) and the environment (e.g. tool use, diet composition).

Social intelligence

In this section, we describe examples that deal with living in individualised groups and corresponding social strategies, social learning and tradition, and co-operative hunting. At the end of this section, we discuss various phenomena found in cleaning symbiosis that indicate that cleaner fish are particularly suited to test the Machiavellian intelligence hypothesis – which states that social complexity causes the enlargement of the neocortex – on fish.

Living in individualised groups

Fish often live in diverse stable groups of varying sizes and sex composition and defend their territories and/or their eggs and larvae. Damselfish of the Red Sea live in individualised social assemblages as pairs, harems, or solitary neighbouring individuals (Fricke 1975a). Cichlids in particular are well known for their uni- or biparental brood care (review: Keenleyside 1991). In a few cases, unrelated and related helpers, which could reproduce themselves, live with the breeding pair (*Lamprologus pulcher*, *L. brichardi*, Taborsky 1984; Grantner and Taborsky 1998). One species, the cichlid *Neolamprologus multifasciatus*, endemic to Lake Tanganyika, lives in extended family groups sensu Emlen (1997), that is, in stable groups with two or more sexually active members of both sexes (Kohler 1997). Individual recognition based primarily on optical cues probably exists in all these stable groups; it has been demonstrated experimentally in a variety of species (Noble and Curtis 1939; Fricke 1973a, 1974; Hert 1985; Balshine-Earn and Lotem 1998). There is even evidence that in damselfish, *Pomacentrus portitus*, individuals recognise each other on purely acoustical cues (Myrberg and Riggio 1985). Kin recognition, based on major histocompatibility complex cues, has been demonstrated in juvenile arctic charr, *Salvelinus alpinus* (Olsen et al. 1998).

Many other fish live in aggregations when not breeding. Most studies have not tested whether fish in such aggregations know each other individually. However, individual recognition must occur in some of these aggregations, according to data on partner choice in foraging situations (review by Dugatkin 1997) and predator inspection behaviour (see below). In summary, individual recognition can safely be assumed to be widespread across fish families, and thus the basis for more complex social behaviour is certainly present in many fish species.

Competing over access to mates

Chance and Mead (1953) have argued that in primates, year-round mating in stable groups might select for individuals that are able to outsmart others. This is because social strategies could have a major influence on reproductive success, as subordinates will try to combine mating success with avoidance of eviction from the group as a consequence of their mating attempts. Such a situation exists in the cichlid fish species with helpers and in the extended family groups of *N. multifasciatus*, and the functional aspects of these conflicts are well studied (Taborsky 1984, 1985; Dierkes et al. 1999). Subordinates' frequent submissive behaviours towards high-ranking group members (Kohler 1997) could be seen as a behavioural adaptation to manipulate the decisions of group members. Wickler (1965, 1969) studied the social behaviour of the cichlid *Tropheus moorei* and found a clear correlation between social rank and frequency of appeasement behaviour. The appeasement behaviours were also used as a different signal during courtship. Wickler (1965) argued that the behaviour of the cichlids was very similar in its evolution and function to the appeasement behaviour of hamadryas baboons, which also has its roots in courtship behaviour and is clearly correlated with rank. Fricke (1974) showed similar relations between appeasement behaviour, dominance, and courtship in anemonefish. Further studies on this topic are clearly needed, both in fish and in primates.

Co-operation

The most famous example of co-operation in fish is probably the inspection of nearby predators by one or several fish that leave the relative safety of their school to do so (Pitcher et al. 1986). During inspection, pairs of sticklebacks, *Gasterosteus aculeatus*, and guppies, *Poecilia reticulata*, among others, approach the predator in alternating moves. A series of experiments led to the conclusion that these fish solve a so-called 'prisoner's dilemma' (Luce and Raiffa 1957). In a prisoner's dilemma, two players have the option of either co-operating or cheating their partner. Cheating the partner yields a higher benefit than co-operation irrespective of what the partner does, but if both partners co-operate they receive a higher benefit than if both cheat, hence the dilemma. Milinski (1987) and Dugatkin (1988) proposed that the fish solve the prisoner's dilemma by playing a 'tit-for-tat'-like strategy, which states that a player starts co-operatively and does in all further rounds what the partner did in the previous round (Axelrod and Hamilton 1981). This interpretation is not yet entirely resolved (see review in Dugatkin 1997) but discussions about the interpretation led to a few experiments with very interesting additional results. Milinski et al. (1990a) could show that individual sticklebacks prefer specific partners to others, which implies that school members recognise each other. In addition, partners build up 'trust' in each other during repeated inspections, that is, they hesitate less in approaching a predator when accompanied by a partner that co-operated in the past (Milinski et al. 1990b). Similar results have been found in guppies (see review in Dugatkin 1997). These data imply that these fish species are capable of bookkeeping (remembering their partners' behaviour during past interactions) with several partners simultaneously. We refer to Dugatkin and Wilson (1993) for ideas about the use of partner-choice situations for cognitive studies.

Information gathering about relationships between other group members

Fish are known to 'eavesdrop' (McGregor 1993), that is, to use information from observations of interactions between conspecifics. Dugatkin and Godin (1992a) provided experimental evidence for female guppies changing their preferences between two males if they observe another female being courted by the less preferred male. Oliveira et al. (1998) showed experimentally that Siamese fighting fish attack 'losers' in a previous fight more vigorously than 'winners', but only if they had witnessed the 'interaction' between the two. (Both fish were actually winners in fights with two other conspecifics that were hidden from the observer's perspective; thus to the observer it looked like the two winners were interacting, and the one that stopped threat behaviour first was the 'loser'.)

Intervening in interactions between other group members

An example of triadic interactions involves recruitment of females into the extended family groups of snail cichlids *N. multifasciatus*. In this species, males prevent other males from entering the group, and females prevent other females from entering the group. However, males could benefit from the presence of additional females, at least under certain circumstances, because it would increase their reproductive success. Schradin and Lamprecht (2000) showed experimentally that males actively intervene in female–female aggression in favour of the unfamiliar female, and that this intervention increased the probability that the new females would settle in the group. Males of the dwarf cichlid, *Apistogramma trifasciatum*, play a similar role (Burchard 1965).

Social learning and tradition

Social learning and traditive behaviour is probably a widespread phenomenon in many species. Coral reef fish repeatedly use specific spawning sites where individuals aggregate far away from their territories or home ranges on the reef. A very prominent case is the migrations of surgeon fish, *Acanthurus nigrofuscus*, in the Red Sea (Fishelson et al. 1986; Myrberg et al. 1988). Fricke (1986a) described shoals of nocturnal sweepers, *Parapriacanthus guentheri*, that use identical resting locations over at least 15 years. Helfman and Schulz (1984) were the first to provide experimental evidence that the repeated use of specific daytime schooling sites and twilight migration routes in French grunts, *Haemulon flavolineatum*, is due to social learning. Translocated individual grunts adopted the behaviour of resident grunts and later performed this behaviour in the absence of the residents, as well. Translocated grunts would not show such behaviour in the absence of trainers. Warner (1988, 1990) studied traditionality in mating site preferences in the blueheaded wrasse, *Thalassoma bifasciatum*. He removed entire populations and replaced them with transplanted individuals. These new individuals established new mating sites, and these mating sites were used long after the initial manipulation. Not once in a 12-year study on 22 patches of reef was a new mating site established apart from the experimental manipulation, providing compelling evidence for the maintenance of mating sites by social learning, rather than through aggregation at sites particularly suited for mating.

More recently, Laland and Williams (1997) conducted laboratory experiments and showed experimentally that guppies learn the way to hidden food sources from knowledgeable conspecifics. The conspecifics had been trained to use only one of two possible ways to the food source. Naïve fish were added and learned the way to the food source by schooling with the others. Members of the original school could be replaced successively and the school still preferentially took the originally learned way to the food source. The fish thus built up a tradition. Using principally the same experimental set up, Laland and Williams (1998) went one step further and showed that even maladaptive behaviour can spread through a population due to social learning. In their study, a longer and therefore more costly way to a foraging site was still preferred over a short way 3 days after all original trainers had been removed.

Another promising case of social learning might be the foraging behaviour in triggerfish, Balistidae. These fish seem to be outstanding in their manipulative behaviours and foraging modes (see also section on foraging skills). They often feed on sea urchins. Usually, they try to ‘blow’ them on their side to get access to the unprotected body parts. Fricke (1971) observed at Eilat how five different individuals of *Balistapus undulatus* successfully hunted sea urchins by first biting off the spines, which allowed them eventually to grab the urchin and take it up close to the surface. They then started feeding from the unprotected underneath while the urchin was slowly dropping down. Despite decades of research on coral reef fish, Fricke has never observed this behaviour anywhere else. The most parsimonious explanation for the repeated occurrence of this behaviour in a refined area is thus social learning.

Another case of interest is the learning of anti-predator behaviour in hatchery fish from tutors (review: Suboski and Templeton 1989). Naïve fish that are given the opportunity to watch a conspecific fleeing from a predator often show an escape response themselves (Magurran and Higham 1988). This process also occurs in mixed-species shoals and can result in the transmission of information between species (Krause 1993). Field studies on this topic still have to be conducted. The adults of some cichlids (e.g. *N. pulcher*) protect their fry against predators (Balshine-Earn et al. 1998). This might help younger group members to learn against which species they should protect their own fry in the future, but this hypothesis remains to be tested. Mobbing is also widespread in fish. Abel (1960) repeatedly witnessed groups of labrids and sparids mobbing an octopus that moved over the bottom; staying close to the octopus and swooping at him they accompanied him until he reached cover. Fricke (1973b) described mobbing behaviour of the three-spotted damselfish, *Dascyllus trimaculatus*, against a variety of predators. Dugatkin and Godin (1992b) provide a review on more recent descriptions of mobbing in fish. As mobbing in birds serves to tell inexperienced birds about predators (Curio et al. 1978), mobbing behaviour in fish should be studied for a similar effect. We use the term ‘effect’ as virtually all coral reef fish species lack brood care and hence do not mob to enhance offspring survival but for other reasons. Still, inexperienced individuals could profit from observations of mobbing behaviour.

There is some evidence that young fish learn what to eat and what to avoid by observing adults. Fish definitely learn horizontally from conspecifics what to eat under lab conditions. Templeton (1987, unpublished PhD thesis, cited in Suboski and Templeton 1989) found that juvenile rock bass, *Ambloplites rupestris*, that saw a trained conspecific eating a novel food item would readily consume that food later when, alone, they were tested for the first time. Without prior observations, these juveniles did not attack the prey over the course of seven daily sessions of 10 min each. LoVullo et al. (1992) provided observations of parental male catfish (*Bagrus meriodionalis*) exposing their broods to invertebrates by spitting the food into the nest. Other likely examples could be the many cases of trophic provisioning in catfish and cichlids (Noakes 1979). Also in coral reefs, some juvenile fish swim with (unrelated) conspecifics after recruitment from their pelagic stage and could therefore also learn what and where to eat by observing conspecifics.

Co-operative hunting

Co-operative hunting has been cited as one of the hallmarks of hominid evolution (see references in Dunbar 1993) and the chimpanzees of Taï became famous because of their sophisticated hunting strategies (Boesch and Boesch 1989). Here, we describe for the first time interspecific co-operative hunting between giant moray eels, *Gymnothorax javanicus*, and red sea coral groupers, *Plectropomus pessuliferus*, or lunartail groupers *Variola louti*, observed at Ras Mohammed National Park, Egypt. It is known that various species of Serranidae opportunistically follow moray eels and octopus when these animals hunt (Diamant and Shpigel 1985). Both moray eels and octopus try to catch prey that hide in caves and tunnels of corals. The prey often has to leave its hiding place in response and is then exposed to the groupers. What makes our observations different is that the two large grouper species mentioned above were observed regularly approaching giant moray eels that were resting in a coral cave and starting to shake their body in exaggerated movements, usually at less than 1 m distance to the moray eel. We saw five different red sea coral groupers show this behaviour 12 times during 523 min of observations, and lunartails showed this behaviour twice during a total of 695 min of observations performed by two different individuals. These data were collected by following individual groupers until they had visited two different cleaning stations (R. Bshary, unpublished data). In 7 of 14 observations, the moray eel left its cave and the two predators would swim next to each other, searching for prey. The groupers would often come so close that the two predators touched each other at their sides. While the moray eels sneaked through holes, the groupers waited above the corals for escaping fish. We also witnessed once how a grouper waited 2 min at a coral head for an escaped prey to come out again, then suddenly swam away about 15 m, started to shake its body in front of a hole, and led a grey moray, *Siderea grisea*, back to the corals where the prey was hidden. Capture of the prey was not observed, however, nor was a successful hunt observed during other joint hunting attempts, or when groupers hunted on their own during the 1,218 min of observations. In conclusion, groupers solicited moray eels to hunt together usually before a prey item was singled out, and they played different roles during the hunt.

Co-operative hunting in the sense that several predators hunt the same prey simultaneously is widespread in fish, especially in mackerels (Carangidae), which have been described herding their prey (Hiatt and Brock 1948; Sette 1950; Hobson 1968). Schmitt and Strand (1982) even argued that in yellowtails, *Seriola lalandei*, individuals play different roles during such hunts (splitting the school of prey, herding the prey) and refrain from single hunting attempts until the prey is in a favourable position. In addition, Schmitt and Strand (1982) mention that the hunting strategies are variable and depend on the prey species. Dugatkin (1997) reviews this study and further examples of social foraging.

A special case of Machiavellian intelligence: deception, punishment, reconciliation, partner choice, and social prestige in cleaning symbiosis

In cleaning symbiosis, so-called client fish trade the removal of parasites and dead or infected tissue against an easy meal for so-called cleaner fish (reviews: Feder 1966; Losey et al. 1999). Cleaning symbiosis is particularly promising for comparative studies as cleaner fish are found in many different fish families and can differ markedly in the degree to which they depend on interactions with clients for their diet (Feder 1966). Full-time cleaners like the cleaner wrasse *Labroides dimidiatus* may have about 2,300 interactions per day with clients belonging to over 100 different species (Grutter 1995).

There is an array of behaviours found in fish (e.g. categorization, cheating, punishment, manipulation through tactile stimulation, altruism) that are also a focus of attention in cognitive studies on primates. (1) There is strong evidence that cleaners can categorise their 100-or-so client species into resident species that have access to their local cleaner only due to their small territory or home range, and other species that have home ranges that cover several cleaning stations. As predicted by biological market theory (Noë et al. 1991), clients with choice options between cleaners almost invariably have priority of access over clients without choice options at cleaning stations (Bshary 2001). This is because clients with choice options would visit another cleaning station instead if they were not inspected soon after arrival at the cleaning station (Bshary and Schäffer 2001). (2) Cleaners regularly cheat their clients, as cleaners can increase their foraging efficiency by feeding on healthy client tissue as well (Bshary and Grutter in press). (3) Clients without choice options often react to cheating by cleaners with aggressive chasing of the cleaner, which is functionally ‘punishment’ (Clutton-Brock and Parker 1995). They terminate the interaction by inflicting costs on the cleaner at their own expense and receive the benefits in the future, as the cleaner will give them (but not other clients that visit in between) a better than average service during their next interaction (Bshary and Grutter in press). According to theory, punishment can function only if there is individual recognition (Ostrom 1990). This suggests that cleaners can distinguish more than 100 individual clients belonging to various species on an individual basis. (4) Cleaners manipulate their clients’ decisions (Bshary and Würth 2001). They do so by providing ‘tactile stimulation’ (Potts 1973), which usually involves hovering above the client and touching the client’s dorsal fin with their pelvic and pectoral fins. Cleaners provide tactile stimulation more often to predatory clients than to harmless clients, which seems to function as pre-conflict management (Aureli and de Waal 2000) to avoid potentially lethal attacks by predators. (5) Cleaners reconcile sensu de Waal and van Rosmalen (1979) with clients that show a negative response (swimming off or aggression) after a cheat by the cleaner, again by using tactile stimulation (Bshary and Würth 2001). Tactile stimulation is either used as an immediate reaction to the client’s behaviour or employed during the next interaction between the cleaner and the very same client it has cheated (Bshary and Würth 2001). (6) Cleaners exploit the presence of a third party to prevent punishing clients from chasing them further. They do this usually (in 5 out of 6 cases observed during a total observation period of 48 h) by starting an interaction – providing tactile stimulation – with a nearby predator, so the aggressive client does not dare to continue its attack. (7) Cleaners behave altruistically towards their clients if bystanders with the option to switch to another cleaning station are present (R. Bshary and A. D’Souza, unpublished data). Cleaners profit from their altruism because clients that visit a cleaning station reproduce the behaviour of the previous client, that is, they invite for inspection if they witnessed a positive interaction and flee from the approaching cleaner if they saw the previous client flee as well. Cleaners thus have a short-term image or social prestige (Alexander 1987; Zahavi 1995; Nowak and Sigmund 1998; Roberts 1998) that determines the probability of getting access to new potential co-operation partners. Though all incoming clients copy the behaviour of the previous clients, cleaner fish behaviour is only influenced by the presence of clients with choice options, while the presence of clients without choice options does not alter their behaviour. Functionally, this makes sense, as the latter will have to come back for inspection anyway, whereas clients with choice options might be a lost food source if they swim off. This result confirms our first point, namely, that cleaners distinguish two classes of client species.

We conclude that there are plenty of seemingly complex (interspecific) social behaviours (cheating, reconciliation, altruism), abilities (species recognition, individual recognition), and concepts (punishment, social prestige, bookkeeping) that can be studied in cleaning symbiosis. It is even more compelling that possible protagonists are found in a variety of fish families and these almost certainly differ in the degree to which they engage in such behaviours, encouraging the use of the comparative approach.

Environmental intelligence

In this section, we describe examples that deal with special foraging skills, tool use, cognitive maps, memory, anti-predator behaviour, and the manipulation of the environment.

Foraging skills

Many fish species probably have very easy daily routines for finding their food, for example, plankton feeders, grazers, and fish predators. The most advanced foraging techniques are probably found in triggerfish, *Pseudobalistes fuscus*, which have developed special techniques for feeding on sea urchins and shellfish. These fish manipulate the environment by removing obstacles to reach hidden (but visible) prey, and experimental evidence suggests that these fish use a well-developed spatial intelligence while trying to get access to their prey (Fricke 1975b). Triggerfish also try to blow water streams to turn sea urchins over, and some individuals of *Balistapus undulatus* were observed cutting the urchins’ spines to be able to lift the prey up (see section on social learning). Wrasses (*Coris angulata*, *Cheilinus fasciatus*, *C. lunulatus*) take sea urchins in their mouth to crush them by swimming against corals to get access to the meat (Fricke 1971; Wirtz 1996). Fricke (1971) even mentioned that these fish swim to the same places within their territories to crush the urchins. This last suggestion warrants further investigation to test whether such places have specific properties and if so, how fish acquire knowledge about what makes a good anvil.

We find it impossible to compare the complexity of fish diets to the complexity of primate diets. Clearly, there are many fish species with a highly diverse diet, which includes algae, corals, plankton, eggs, and a variety of invertebrates (Hiatt and Strasburg 1960; Vivien 1973; Hobson 1974). The important unsolved question is whether these fish feed selectively on some algae, coral, and invertebrate species, just as primates feed selectively on the leaves and fruits of a few tree species. Without selectivity, the diets of these fish species would be diverse but not complex. There is some evidence that grazing fish species indeed feed selectively on some algae species (Ogden and Lobel 1978). These fish thus must make decisions about what to eat and where, and they would profit from remembering when they last visited a food patch to avoid visits to one recently depleted. This topic clearly needs further study.

Tool use

The use of an anvil to crush shellfish as described above is clearly a case of substrate use. It does not hold up, however, to the restrictive definition of tool use – that an animal must directly handle an agent to achieve a goal (Beck 1980). An example that more closely fits the strict definition is the use of leaves as tablets for carrying eggs to safety when disturbed, as has been documented in South American cichlids (Timms and Keenleyside 1975; Keenleyside and Prince 1976). The catfish *Hoplosternum thoracatum* also has its eggs glued to leaves and with this ‘baby carriage’ may bring them into its foam nest if the leave gets detached (Armbrust 1958).

Spatial memory

There are plenty of potential examples of fish using cognitive maps that may hold up after critical re-examination. The best example is perhaps the behaviour of intertidal gobies, for example, *Gobius soporator*. During low tide, these fish stay in tide pools, but they can jump from one tide pool to another without being able to see the second pool at the onset of the jump. They even jump through a series of pools and escape to the sea if the one they are in is drying out or if a human experimenter harasses them. It has been shown in experiments that this fish swims over the tide pools at high tide and acquires an effective memory of the topography around the home pool. They will not leave their tide pool if they are translocated into a new area that they have never inspected during high tide (Aronson 1951, 1956). A similar escape behaviour from tide pools has been described by Mast (1915) for *Fundulus*, a cyprinodont fish.

Careful observations by Guitel (1893) suggest that some small blenniid fish use landmarks in their nesting area for homing. Fricke (1974) showed experimentally that anemonefish, *Amphiprion bicinctus*, use landmarks to find their host anemone. He caught the fish and kept them at another location for 6 months. He then released them near their original anemone, which was out of sight. The fish swam immediately to the anemone while strangers did not. Other potential examples of highly developed spatial skills are the spawning migrations (Helfman and Schulz 1984; Fishelson et al. 1986) and the fast learning of territory boundaries by a new partner after the removal of one pair member in butterflyfish, *Chaetodon chrysurus* (Fricke 1986b).

Long-term memory

Fricke (1974) examined memory in a social context. He presented anemonefish, *A. bicinctus*, with a conspecific in a Plexiglas aquarium for 1 h. Initially, anemonefish defended their anemone and were aggressive towards conspecifics but stopped this behaviour within the 1-h exposure. The anemone owner was translocated (to avoid site familiarity) and still recognised the individual in the Plexiglas tube after 30 days against alternative partners (Wilcoxon test, n=12, T=6.5, P<0.01; P value not calculated in original study).

Spatial information seems to be stored for long time periods as well. Goldsmith (1914) proved precise spatial memory for more than 18 days in a goby, *Gobius minutus*. The gobies in Aronson's (1951, 1956) experiments remembered the location of tide pools over periods of 40 days without additional experience at high tide, and the anemonefish (Fricke 1974) remembered landmarks for at least 6 months (see section on spatial memory).

Cyprinid fish, *Scardinius erythrocephalus* and *Squalius cephalus*, in Lago Maggiore, which were habituated by a M.S. May to feed from his mouth and hands did so again within 3 min after a 6-month break (Klausewitz 1960). The fish would only accept him and not strangers.

Fricke (1975b) examined how long a fish would remember a food item that was hidden before its eyes. Trigger fish stayed close and examined the hiding place for more than 3 min. For comparison, a horse tested under similar conditions remembered a hidden food item for just 6 s, a dog for 63 min (Grizmek 1944).

Manipulation of the environment

Surprisingly, primates hardly manipulate their environment, a feature that is so obviously important in human societies. An exception is the nest building of the great apes (review by Fruth and Hohmann 1996). Fish seem to be much more skilful in this respect. There are at least 9,000 fish species that build some kind of nest (Paxton and Eschmeyer 1998). Many fish species build nests either for egg laying or for shelter against predators. The nests vary in their complexity from simple burrows to extremely complex structures. A male *Exoglossum* minnow carefully selects more than 300 same-sized stones from over 5 m distance to build a spawning mound 35 cm wide and 10 cm high (van Duzer 1939). Another cyprinid fish builds dome-shaped stone nests from 10,000 pebbles (Lachner 1952).

The most famous example of a shelter-building fish is the jawfish, *Opistognathus aurifrons*. These fish collect stones of various sizes to build a wall that closes the gap of a hole to a size that permits them just to go through. The building of the wall involves repeated rearrangement of the stones and interruption of the work to search for new stones that might fit the gap better than the ones that are lying nearby (Kacher 1963; Colin 1972). Colin (1973) describes the building of the burrow and the flexibility in behavioural sequences under natural conditions in great detail.

Impressive coral mounts of 90–300 cm length and 40–80 cm height are constructed by the sand tile fish, *Hoplolatilus geo*, which live pairwise in colonies in deep water of the Red Sea. These fish selectively collect 3- to 5-cm coral pebbles and use them as building fragments to pile up one of the biggest constructions with foreign materials known in fish (Fricke and Kacher 1982).

Fish from various taxonomic families build nests from plant material that they collect and transport to a chosen place where they push and stick the material together to form a solid mass. Most famous is the dextrous nest-building behaviour of the ten-spined stickleback, *Pygosteus pungitius* (Leiner 1931), which is clearly flexible depending on the environmental situation. For example, although the nest is usually built before the female lays her eggs, egg laying can also happen first and the male will afterwards build the nest around the eggs. This has to be done in a very different way to avoid damaging the eggs (which the males obviously achieve, as those eggs do hatch; Morris 1958).

Discussion

Our list of phenomena observed in fish clearly shows that fish as a taxon have found solutions to almost all the problems that supposedly led to the evolution of a large neocortex and cognitive skills in primates. Some examples even suggest that fish might use similar mechanisms to solve these problems, though this should be carefully reexamined in future research. We believe that many other examples of cognitive skills existent in fish await description by scientists.

The most obvious difference, at least according to our present knowledge, between any primate species and fish as a taxon is the evidence of selective foraging in primates. Here we see a huge potential for learning from conspecifics (most likely the mother) what to eat and what to avoid, though there is still a lack of empirical evidence on how primates acquire such knowledge. The differences in diet complexity between fish and primates support the hypothesis that the enlargement of the neocortex in primates was caused by the demands of a complex diet (Clutton-Brock and Harvey 1980), for which there is some recent evidence (Barton 1995; Barton and Dunbar 1997). Still, this conclusion is very preliminary as this topic has hardly been investigated in fish, and it is therefore unclear whether the difference is real or due to a lack of knowledge. Foraging innovations in guppies, for example, spread readily through a population under controlled laboratory conditions (Laland and Reader 1999).

For the time being, we consider it extremely unlikely that members of large shoals of fish know each other on an individual basis. Thus, large individualised groups do not seem to occur in fish, and hence the selective advantages of having social skills are generally lower in fish than in primates. Still, the data on predator inspection behaviour suggest that fish species with the tendency of shoaling know some group members individually, and the individualised helper systems and extended family groups of cichlids are comparable in size to some primate species. In cleaning symbiosis, as well, there is a very large network of cleaners and clients, especially from the cleaners' perspective. For cleaners, this network is larger than group sizes of any primate species, and species recognition and individual recognition seem to occur at least to some extent. Not surprisingly, it is in cleaning symbiosis where we find many social behaviours that are the focus of attention in the Machiavellian intelligence hypothesis (Byrne and Whiten 1988).

There are two interesting primate behaviours of which we did not find evidence in fish. First, there are no within-group coalitions described in fish, whereas nepotistic coalitions in primates are very common (see examples in Harcourt and de Waal 1992), and the coalition formation between unrelated male savannah baboons, *Papio anubis*, has been studied in detail (Noë 1990). Second, there is still a lack of evidence that tactical deception occurs in fish. However, tactical deception cannot be seen as a general feature of primate species as evidence is limited to a few species (Byrne and Whiten 1988), and there are doubts whether tactical deception reflects complex strategic thinking or basic operant learning (Heyes 1998).

Having established that most problems that primates face and solve in their daily life exist in fish as a taxon, it is worth looking at the species level. While one can assume that any primate (species) might be able to use the entire set of social and environmental skills that are investigated here, such a statement seems to be less obvious for fish. Our examples were chosen from a variety of fish species, not because we wanted to include examples of as many fish families as possible but because we had to in order to cover all skills. In principle, it could be that this just reflects the low investment in studies on fish cognition. Still, for the time being, we hypothesise that the diversity of skills found in individual primates as opposed to individual fish might reflect the major difference between the two taxa. Assuming that every additional skill needs an increase in neocortex size, the additive effects of computational power might even have led to fulguration (Lorenz 1973), the occurrence of a new system of traits that is not predictable from the traits themselves. Probably the most prominent topics in this context are currently theory of mind (Premack and Woodruff 1978) and imitation learning (Whiten et al. 1996).

Based on our list of examples, we see three good reasons why cognitive research can profit from including fish as study animals. First, ecological factors that might select for cognitive skills are relatively easy to identify. Second, links between cognitive skills and brain anatomy are relatively easy to identify. Third, decision rules used by fish can be used to generate null hypotheses for decision rules used by primates. We will now elaborate on these three aspects.

The link between ecology and cognitive skills

It should be much easier to identify the selective pressures that led to the evolution of specific cognitive skills in fish than in primates. This is because each interesting phenomenon usually occurs in a few fish species only, and closely related species might lack the feature in question. This applies to both social and environmental skills. Comparisons of closely related fish species that differ in their ecology are thus numerous and easy to find to test for differences in specific cognitive skills. Primates, on the other hand, are supposedly much more uniform with respect to many features of interest. For instance, virtually all diurnal primates live in permanent individualised groups (though of varying structures).

Maybe the best-studied case to date of the 'ecological intelligence' approach that we want to promote is the link between food-caching behaviour and spatial memory in birds. Kamil and colleagues have shown that bird species that rely heavily on caching food for their winter diet have a better spatial memory than non-caching or less-caching species, but there is no difference between these species in operant tests (review in Kamil 1998; Balda and Kamil 1998). Specific selection pressures really can lead to highly advanced cognitive abilities in species that are supposed to be generally more primitive than primates.

The link between cognitive skills and brain anatomy

Again, fish show a great variety in their ecology, even between closely related species, and most species lack the cognitive skills that are of interest for primatologists. It will therefore be relatively easy to compare the brain anatomy of two closely related species, of which one shows a specific cognitive ability while the other does not.

Also, the importance of ontogenetic effects on brain anatomy can be studied in fish. These effects are particularly well studied in food-caching behaviour in birds (review in Clayton and Lee 1998). Still, fish are also very suitable to study effects of ontogeny, as fish can generate new brain cells during their entire life, in contrast to mammals (review in Kotrschal et al. 1998). Fish are usually easy to keep in the lab, so large sample sizes can be obtained from individuals raised in a variety of environments that, for example, differ in social complexity. Regulations for experiments and for the collection of brain samples are easier to fulfil than in other vertebrate taxa.

A limitation on the value of studies on the link between cognitive abilities and brain anatomy in fish for studies on other vertebrate taxa might occur because fish might use non-homologous brain areas to solve some cognitive problems. For example, Healey (1957) wrote that the mesencephalon of fish is a region where incoming messages are received and translated into appropriate messages to the effector system. In addition, it appears to be involved in learning. Still, there is evidence that the telencephalon of fish is also used to co-ordinate lower functions. For example, three-spined sticklebacks, *Gasterosteus aculeatus*, can perform all behaviours connected to nest building when the telencephalon is lesioned, but not in a sequence that would lead to the actual building of a nest (Schönherr 1954; Segaar 1956). A very promising result comes from a comparison of the relative sizes of various brain parts in different fish species, published by Geiger (1956). He found that triggerfish, which have advanced foraging techniques, have a relatively larger telencephalon than most other families investigated.

There have been several attempts to link the ecology of fish species with brain size (review by Kotrschal et al. 1998). Again, the conclusions are very promising. Cichlids of the East African Lakes vary greatly in their telencephalon size (van Staaden et al. 1995). Cichlids are probably the most promising fish family to study the relation between social organisation and brain anatomy, because of the large interspecific variance in the amount of brood care, which leads to extended family groups in *Neolamprologus multifasciatus*. In addition, cichlids also live in a great variety of habitats, and van Staaden et al. (1995) and Huber et al. (1997) found a strong link between forebrain size and spatial complexity of the habitat, as it had been claimed earlier for primates (Clutton-Brock and Harvey 1980). What is still missing is to link such information on fish ecology and brain structure with cognitive skills.

Cognitive skills of fish as ‘null hypotheses’ for primate behaviour

Standards in cognitive research have been raised as a result of criticism from Heyes (1993, 1994), who pointed out that many supposed examples of theory of mind and imitation learning in primates could be explained with simpler mechanisms, for example, stimulus enhancement. Recently researchers have explicitly tried to design experimental setups that allowed them to distinguish between imitation learning and stimulus enhancement (Whiten et al. 1996), but it might be difficult to come up with simple explanations as ‘null hypotheses’ for observed behavioural skills. This is where we think that primatology can profit directly from cognitive research in other, supposedly less sophisticated taxa like fish. Determining the decision rules used by fish, for example, would provide a supposedly simple rule for how animals might tackle a problem. These decision rules could then be used to interpret primate behaviour and would have to be expanded only if they did not suffice to describe primate behaviour accurately. If primates use more complex decision rules to solve similar problems, one can start looking at the details of the behaviours to see whether the more complex rules yield specific advantages. This suggestion is based on the assumption that fish and primates often use the same cognitive mechanisms to solve problems. Although we have limited our article to a discussion of behavioural phenomena, the comparative cognition literature on controlled laboratory experiments suggests that this a reasonable assumption (Macphail 1982, 1985). Because of these similarities, Macphail (1982) even suggested his ‘null hypothesis’ that there are neither qualitative nor quantitative differences between the cognitive abilities of any vertebrate species. Only humans are special because of their well-developed language. This extreme approach certainly does not hold up in light of current evidence (Macintosh et al. 1985; Balda and Kamil 1998), but the notion that differences are quantitative rather than qualitative, at least among vertebrates, seems fairly solid. We are aware of only one experimentally shown qualitative difference in mechanisms between primates and fish, and this difference is the ability to imitate (Whiten et al. 1996; Voelkl and Huber 2000).

We want to illustrate our point with a discussion of decision rules that could be used in the context of co-operation and cheating. It might turn out that in cleaning symbiosis, fish use just the outcome (positive or negative) of the last interaction to make a decision about present behaviour. In contrast, the behaviour of primates towards group members might depend on a long history of previous interactions rather than on just their last one. Could such a more complex decision rule yield benefits? Milinski and Wedekind (1998) have shown that humans who are confronted with a simple iterated prisoner’s dilemma game (Axelrod and Hamilton 1981) use knowledge of their partners’ and their own decisions (co-operate or defect) gathered over several rounds to decide on their present move. Using such complex information, humans were more successful in this game than if they had used simple 'tit-for-tat-like strategies (do what your partner did in the last round) or Pavlovian strategies (if you receive a high payoff then repeat your behaviour; if you receive a low payoff then switch behaviour).

Promising study systems

Where should one begin in an area hardly anybody else is working on at the same taxonomic level? We emphasise once again that almost all the phenomena we described await detailed analysis of underlying mechanisms and hence offer a promising starting point. The East African Lake cichlids might be most similar to primates in that the effects of both social and environmental complexity can be studied in the same systems. As brood care is widely abundant in these species, juveniles might have the option to learn what to eat by following their parents. Social competence will be important in species with helper systems, as helpers will try to combine achievement of direct fitness benefits and avoidance of being evicted from the group. Triggerfish and wrasses are likely candidates to study foraging skills, and a variety of reef fish should have highly developed spatial skills. The most promising candidates to study social intelligence are cleaner fish. Cleaners are found in a variety of fish families, and species differ widely in the degree to which they depend on cleaning for their diet (reviews in Feder 1966). This should have led to strong variance in (interspecific) social skills, which cleaners use to improve their foraging efficiency. For example, tactile stimulation, which the cleaner wrasse *Labroides dimidiatus* uses in a variety of circumstances to manipulate clients' behaviour (Bshary and Würth 2001), has so far only been described for 'full-time' cleaners from the genus *Labroides*. But there is also within-species variance in the degree of co-operation, depending on ecological conditions. For example, Grutter (1997) found that *L. dimidiatus* fed almost exclusively on parasitic isopods around Lizard Island but ate much more mucus around Heron Island at the southern end of the Great Barrier Reef. Full-time cleaners will probably turn out to be the ultimate Machiavellian strategists among fish. *L. dimidiatus* has 1,000–2,300 interactions per day with clients belonging to sometimes over 100 species (Grutter 1996; R. Bshary, unpublished data), and cheating, punishment, and reconciliation occur about 50–200 times a day (R. Bshary, unpublished data). The clients' perspective in cleaning symbiosis might be interesting as well. Individual recognition, spatial memory for the locations of cleaning stations, punishment, partner switching, bookkeeping – all these aspects might be elaborated to varying degrees. Cleaning symbiosis and predator inspection are extremely promising systems to combine evolutionary game theory and learning (see Stephens and Clements 1998). Finally, zebrafish could provide the best study system to investigate the interaction between genes and behaviour, as they are a model system for geneticists. For example, there are studies on how gene mutations affect brain development (Brand et al. 1996), and such knowledge could be used for a cognitive approach on the behavioural level.

In conclusion, we believe that future studies on cognitive skills in fish will yield both exciting insights into specific abilities of at least some fish species and a sharper view on why primates might be as special as most of us think they are. The differences from other taxa might often turn out to be quantitative rather than qualitative.

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References

Abel EF (1960) Zur Kenntnis des Verhaltens und der Ökologie von Fischen an Korallenriffen bei Ghardaqa (Rotes Meer). Z Morph Ökol Tiere 49:430–503

Alexander RD (1987) The biology of moral systems. Aldine de Gruiter, New York

Armbrust W (1958) Haltung und Zucht von *Hoplosternum thoracatum*. Aquar Terr Z 11:97–100

Aronson LR (1951) Orientation and jumping behavior in the gobiid fish *Bathygobius soporator*. Am Mus Novitates 1486

Aronson LR (1956) Further studies on orientation and jumping behavior in the goby fish, *Bathygobius soporator*. Anat Rec 125:606

Aureli F, de Waal FBM (2000) Natural conflict resolution. Cambridge University Press, Cambridge

Axelrod R, Hamilton WD (1981) On the evolution of cooperation. Science 211:1390–1396

Balda RP, Kamil AC (1998) The ecology and evolution of spatial memory in corvids of the southwestern USA: the perplexing pinyon jay. In: Balda RP, Bednekoff PA, Kamil AC (eds) Animal cognition in nature. Academic Press, New York, pp 29–64

Balda RP, Bednekoff PA, Kamil AC (eds) (1998) Animal cognition in nature. Academic Press, New York

Balshine-Earn S, Lotem A (1998) Individual recognition in a cooperatively breeding cichlid: evidence from video playback experiments. Behaviour 135:369–386

Balshine-Earn S, Neat FC, Reid H, Taborsky M (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behaviour in a cooperatively breeding fish. Behav Ecol 9:432–438

Barton RA (1995) Neocortex size and behavioural ecology in primates. Proc R Soc Lond B 263:173–177

Barton RA, Dunbar RIM (1997) Evolution of the social brain. In: Whiten A, Byrne DW (eds) Machiavellian intelligence II. Cambridge University Press, Cambridge, pp 240–263

Beck B (1980) Animal tool use behaviour: the use and manufacture of tools by animals. Garland STPM Press, New York

Boesch C, Boesch H (1989) Hunting behaviour of wild chimpanzees in the Taï National Park. Am J Phys Anthropol 78: 547–573

Brand M, Heisenberg C-P, Jiang Y-J, Beuchle D, Lun K, Furutani-Seiki M, Granato M, Haffter P, Hammerschmidt M, Kane DA, Kelsh RN, Mullins MC, Odenthal J, Eeden FJM van, Nuesslein-Volhard C (1996) Mutations in zebrafish genes affecting the formation of the boundary between midbrain and hindbrain. Development 123:179–190

Bshary R (2001) The cleaner fish market. In: Noë R, Hooff JARAM van, Hammerstein P (eds) Economics in nature. Cambridge University Press, Cambridge, pp 146–172

Bshary R, Grutter AS (in press) Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. Anim Behav

Bshary R, Schäffer D (2001) Choosy reef fish select cleaner fish that provide high service quality. Anim Behav (in press)

Bshary R, Würth M (2001) Cleaner fish, *Labroides dimidiatus*, manipulate client reef fish by providing tactile stimulation. Proc R Soc Lond B 268:1495–1501

Burchard JE (1965) Family structure in the dwarf cichlid *Apistogramma trifasciatum*. Z Tierpsychol 22:150–162

Byrne RW, Whiten A (eds) (1988) Machiavellian intelligence. Clarendon Press, Oxford

Chance M, Mead A (1953) Social behaviour and primate evolution. Symposia of the Society for Experimental Biology. Evolution 7:395–439

Clayton NS, Lee DW (1998) Memory and the hippocampus in food-storing birds. In: Balda RP, Bednekoff PA, Kamil AC (eds) Animal cognition in nature. Academic Press, New York, pp 99–118

Clutton-Brock TH, Harvey PH (1980) Primates, brain and ecology. J Zool (Lond) 190:309–323

Clutton-Brock TH, Parker GA (1995) Punishment in animal societies. Nature 373:209–215

Colin PL (1972) Daily activity patterns and effects of environmental conditions on the behavior of the yellowhead jawfish, *Opisthognathus aurifrons*, with notes on its ecology. Zoologica 57:137–169

Colin PL (1973) Burrowing behaviour of the yellowhead jawfish, *Opistognathus aurifrons*. Copeia 1973:84–90

Curio E, Ernst U, Vieth W (1978) The adaptive significance of avian mobbing II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. Z Tierpsychol 48:184–202

de Waal FBM, Roosmalen A van (1979) Reconciliation and consolation among chimpanzees. Behav Ecol Sociobiol 5:55–66

Diamant A, Shpigel M (1985) Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the gulf of Eilat (Aqaba). Environ Biol Fish 13:153–159

Dierkes P, Taborsky M, Kohler U (1999) Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behav Ecol 10:510–515

Dugatkin LA (1988) Do guppies play Tit for Tat during predator inspection visits? Behav Ecol Sociobiol 25:395–399

Dugatkin LA (1997) Cooperation among animals. Oxford University Press, New York

Dugatkin LA, Godin J-GJ (1992a) Reversal of female mate choice by copying in the guppy *Poecilia reticulata*. Proc R Soc Lond B 249:179–184

Dugatkin LA, Godin J-GJ (1992b) Prey approaching predators: a cost-benefit perspective. Ann Zool Fennici 29:233–252

Dugatkin LA, Wilson DS (1993) Fish behaviour, partner choice and cognitive ethology. Rev Fish Biol Fish 3:368–372

Dunbar RIM (1992) Neocortex size as a constraint on group size in primates. J Hum Evol 20:287–296

Dunbar RIM (1993) Coevolution of neocortical size, group size and language in humans. Behav Brain Sci 16:681–735

Duzer EM van (1939) Observations on the breeding habits of the cut-lip minnow, *Exoglossum maxillingua*. Copeia 1939:65–75

Emlen ST (1997) Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB (eds) Behavioural ecology, 4th edn. Blackwell, Oxford, pp 228–253

Feder HM (1966) Cleaning symbiosis in the marine environment. Symbiosis 1:327–380

Fishelson L, Montgomory LW, Myrberg AA (1986) Social biology and ecology of acanthurid fish near Eilat (Gulf of Aqaba, Red Sea). In: Indopacific fish biology, Proceedings of the Second International Conference on Indo-Pacific Fishes, pp 938

Fricke H (1971) Fische als Feinde tropischer Seeigel. Mar Biol 9:328–338

Fricke H (1973a) Individual partner recognition in fish: field studies on *Amphiprion bicinctus*. Naturwissenschaften 60:204–205

Fricke H (1973b) Ökologie und Sozialverhalten des Korallenbarsches *Dascyllus trimaculatus* (Pisces, Pomacantridae). Z Tierpsychol 32:225–256

Fricke H (1974) Öko-Ethologie des monogamen Anemonenfisches *Amphiprion bicinctus*. Z Tierpsychol 36:429–512

Fricke H (1975a) Sozialstruktur und oekologische Spezialisierung von verwandten Fischen (Pomacentridae). Z Tierpsychol 39: 492–520

Fricke H (1975b) Lösen einfacher Probleme bei einem Fisch. Z Tierpsychol 38:18–33

Fricke H (1986a) *Parapriacanthus guentheri* – Schwarmverhalten (Freiwasseraufnahmen). Publ Wiss Film Sekt Biol Ser 18, Nr 1/E2185

Fricke H (1986b) Pair swimming in monogamous butterflyfish: a joint advertisement for territory. Ethology 73:307–333

Fricke H, Kacher H (1982) A mound-building deep water sand tilefish of the Red Sea: *Hoplolatilus geo* n. sp. (Perciformes: Branchiostegidae). Observations from a research submersible. Senckenbergiana Marit 14:245–259

Fruth B, Hohmann G (1996) Nest building behaviour in the great apes: the great leap forward? In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 225–240

Geiger W (1956) Quantitative Untersuchungen über das Gehirn der Knochenfische, mit besonderer Berücksichtigung seines relativen Wachstums, I. Acta Anat 26:121–163

Goldsmith M (1914) Les reactions physiologiques et psychiques des poissons. Bull Inst Gén Psychol 14:97–228

Grantner A, Taborsky M (1998) The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher*. J Comp Psychol 168:427–433

Grizmek B (1944) Gedächtnisversuche mit Pferden. Z Tierpsychol 6:445–454

Grutter AS (1995) Relationship between cleaning rates and ectoparasite loads in coral reef fishes. Mar Ecol Prog Ser 118:51–58

Grutter AS (1996) Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. Mar Ecol Prog Ser 130:61–70

Grutter AS (1997) Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. Copeia 1997:346–355

Guitel F (1893) Observations sur les moeurs de trois blenniidés (*Clinus argentatus*, *Blennius montagui*, *B. sphynx*). Arch Zool Exp 1893, sér III:325–384

Harcourt AW, de Waal FBM (eds) (1992) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford

Healey EG (1957) The nervous system. In: Brown ME (ed) The physiology of fishes, vol 2. Academic Press, New York, pp 1–119

Helfman GS, Schultz ET (1984) Social transmission of behavioural traditions in a coral reef fish. Anim Behav 32:379–384

Helfman GS, Colette BB, Facey DE (1997) The diversity of fish. Blackwell Science, Malden, Mass.

Hert E (1985) Individual recognition of helpers by the breeders in the cichlid fish *Lamprologus brichardi* (Poll, 1974). Z Tierpsychol 68:313–325

Heyes CM (1993) Imitation, culture and tradition. Anim Behav 46:999–1010

Heyes CM (1994) Reflections on self-recognition in primates. Anim Behav 47:909–919

Heyes CM (1998) Theory of mind in non human primates. Behav Brain Sci 21:101

Hiatt RW, Brock VE (1948) On the herding of prey and the schooling of the black skipjack, *Euthynnus yaito* Kishinouye. Pac Sci 2:297–298

Hiatt RV, Strasburg DV (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30:65–127

Hobson ES (1968) Predatory behavior of some shore fishes in the Gulf of California. U S Fish Wildl Serv Res Rep 73:1–92

Hobson ES (1974) Feeding relationships of teleost fishes on coral reefs in Kona, Hawaii. Fish Bull 27:915–1031

Huber R, Staaden MJ van, Kaufman LS, Liem KF (1997) Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. BBE 50:167–182

Humphrey NK (1976) The social function of intellect. In: Bateson PP, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317

Jerison HJ (1985) Animal intelligence and encephalization. Philos Trans R Soc Lond B Biol Sci 308:21–35

Kacher H (1963) *Opithognathus aurifrons* (Opisthognathidae) – Graben einer Wohnhöhle, Wallbau Film E514, Encyclopaedia Cinematographica. Institut für den wissenschaftlichen Film, Göttingen

Kamil AC (1998) On the proper definition of cognitive ethology. In: Balda RP, Bednekoff PA, Kamil AC (eds) Animal cognition in nature. Academic Press, New York, pp 1–28

Keenleyside MHA (ed) (1991) Cichlid fishes. Chapman & Hall, London

Keenleyside MHA, Prince CE (1976) Spawning-site selection in relation to parental care of eggs in *Aequidens paraguayensis* (Pisces: Cichlidae). Can J Zool 54:2135–2139

Klausewitz W (1960) Ein bemerkenswerter Zähmungsversuch an freilebenden Fischen. Natur Volk 90:91–96

Kohler U (1997) Zur Struktur und Evolution des Sozialsystems von *Neolamprologus multifasciatus* (Cichlidae, Pisces), dem kleinsten Schneckenbuntbarsch des Tanganjikasees. PhD thesis, Ludwig-Maximilian-Universität, Munich

Kotrschal K, Staaden MJ van, Huber R (1998) Fish brains: evolution and environmental relationships. Rev Fish Biol Fish 8: 373–408

Krause J (1993) Transmission of fright reaction between different species of fish. Behaviour 127:37–48

Lachner A (1952) Studies of the biology of the cyprinid fish of the chub genus *Nocomis* of northeastern United States. Am Midl Nat 48:433–466

Laland KN, Reader SM (1999) Foraging innovation in the guppy. Anim Behav 57:331–340

Laland KN, Williams K (1997) Shoaling generates social learning of foraging information in guppies. Anim Behav 53:1161–1169

Laland KN, Williams K (1998) Social transmission of maladaptive information in the guppy. Behav Ecol 9:493–499

Leiner M (1931) Ökologisches von *Gasterosteus aculeatus* L. Ergänzende Mitteilungen zu den Abhandlungen von W. Wunder und M. Leiner. Zool Anz 93:317–333

Lorenz K (1973) Die Rückseite des Spiegels. Versuch einer Naturgeschichte menschlichen Erkennens. Piper, Munich

Losey GC, Grutter AS, Rosenquist G, Mahon JL, Zamzow JP (1999) Cleaning symbiosis: a review. In: Almada VC, Oliveira RF, Goncalves EJ (eds) Behaviour and conservation of littoral fish. Instituto Superior de Psicologia Aplicada, Lisbon, pp 379–395

LoVullo TJ, Stauffer JR, McKaye KR (1992) Diet and growth of a brood of *Bagrus meridionalis* (Siluriformes: Bagridae) in Lake Malawi, Africa. Copeia 1992:1084–1088

Luce RD, Raiffa H (1957) Games and decisions. Wiley, New York

Macintosh NJ, Wilson B, Boakes RA (1985) Differences in mechanisms of intelligence among vertebrates. Philos Trans R Soc Lond B Biol Sci 308:53–65

Macphail EM (1982) Brain and intelligence in vertebrates. Oxford: Clarendon Press

Macphail EM (1985)Vertebrate intelligence: the null hypothesis. Philos Trans R Soc Lond B Biol Sci 308:37–51

Magurran AE, Higham A (1988) Information transfer across fish shoals under predator threat. Ethology 78:153–158

Marler PK (1996) Are primates smarter than birds? In: Nolan V, Ketterson ED (eds) Current ornithology. Plenum Press, New York, 1–32

Mast SO (1915) The behavior of *Fundulus*, with special reference to overland escape from tide-pools and locomotion on land. Anim Behav 5:341–350

McGregor PK (1993) Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. Philos R Soc Lond B Biol Sci 340:237–244

Milinski M (1987) Tit for tat in sticklebacks and the evolution of cooperation. Nature 325:433–435

Milinski M, Wedekind C (1998) Working memory constrains human cooperation in the prisoner's dilemma. Proc Natl Acad Sci U S A 95:13755–13758

Milinski M, Külling D, Kettler R (1990a) Tit for tat: sticklebacks *Gasterosteus aculeatus* 'trusting' a cooperative partner. Behav Ecol 1:7–11

Milinski M, Pfluger D, Külling D, Kettler R (1990b) Do sticklebacks cooperate repeatedly in reciprocal pairs? Behav Ecol Sociobiol 27:17–21

Morris D (1958) The reproductive behaviour of the ten-spined stickleback (*Pygosteus pungitius* L.). Behaviour [Suppl] 6:1–154

Myrberg AA, Riggio RJ (1985) Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus portitus*). Anim Behav 33:411–416

Myrberg AA, Montgomery WL, Fishelson L (1988) The reproductive behaviour of *Acanthurus nigrofuscus* (Forskal) and other surgeon fishes (Fam. Acanthuridae) of Eilat, Israel (Gulf of Aqaba, Red Sea). Ethology 79:31–61

Noakes DL (1979) Parent-touching behaviour by young fishes: incident, function and causation. Environ Biol Fish 4:389–400

Noble GK, Curtis B (1939) The social behaviour of the jewel fish, *Hemichromis bimaculatus* Gill. Bull Am Mus Nat Hist 76:1–46

Noë R (1990) A veto game played by baboons: a challenge to the use of the prisoner's dilemma as a paradigm for reciprocity and cooperation. Anim Behav 39:78–90

Noë R, Schaik CP van, Hooff JARAM van (1991) The market effect: an explanation for pay-off asymmetries among collaborating animals. Ethology 87:97–118

Nowak MA, Sigmund K (1998) Evolution of indirect reciprocity by image scoring. Nature 393:573–577

Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. Environ Biol Fish 3:49–63

Oliveira RF, McGregor PK, Latruffe C (1998) Know thine enemy: fighting fish gather information from observing conspecific interactions. Proc R Soc Lond B 265:1045–1049

Olsen KH, Grahn M, Lohm J, Langefors A (1998) MHC and kin recognition in juvenile arctic charr, *Salvelinus alpinus* (L.). Anim Behav 56:319–327

Ostrom E (1990) Governing the commons: the evolution of institutions for collective action. Cambridge University Press, New York

Paxton JR, Eschmeyer WN (1998) Encyclopedia of fishes. Academic Press, San Diego, Calif.

Pitcher TJ, Green DA, Magurran AE (1986) Dicing with death: predator inspection behavior in minnow *Phoxinus phoxinus* shoals. J Fish Biol 28:439–448

Potts GW (1973) The ethology of *Labroides dimidiatus* (Cuv. and Val.) (Labridae, Pisces) on Aldabra. Anim Behav 21:250–291

Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? Behav Brain Sci 4:515–526

Roberts G (1998) Competitive altruism: from reciprocity to the handicap principle. Proc R Soc Lond B 265:427–431

Schmitt RJ, Strand SW (1982) Cooperative foraging by yellowtail *Seriola lalandei* (Carangidae) on two species of fish prey. Copeia 1982:714–717

Schönherr J (1954) Über die Abhängigkeit der Instinkthandlungen vom Vorderhirn und Zwischenhirn (Epiphyse) bei *Gasterosteus aculeatus* L. Zool Jahrb Abt Allg Zool Physiol 65:357–386

Schradin C, Lamprecht J (2000) Female-biased immigration and male peace-keeping in groups of the shell-dwelling cichlid fish *Neolamprologus multifasciatus*. Behav Ecol Sociobiol 48:236–242

Seegar J (1956) Brain and instinct with *Gaterosteus aculeatus*. Proc K Ned Wet Amst C59:738–749

Sette OE (1950) Biology of the Atlantic mackerel (*Scomber scombrus*) of North America II – migration and habits. Fish Bull 49, U S Fish Wildl Serv 51:251–358

Shettleworth SJ (1998) Cognition, evolution, and behaviour. Oxford University Press, New York

Staaden MJ van, Huber R, Kaufman L, Liem K (1995) Brain evolution in cichlids of the African Great Lakes: brain and body size, general patterns and evolutionary trends. Zoology 98: 165–178

Stephens DW, Clements KC (1998) Game theory and learning. In: Dugatkin LA, Reeve HK (eds) Game theory and animal behaviour. Oxford University Press, Oxford, pp 239–260

Suboski MD, Templeton JJ (1989) Life skills training for hatchery fish: social learning and survival. Fish Res 7:343–352

Taborsky M (1984) Broodcare helpers in the cichlid fish, *Lamprologus brichardi*: their costs and benefits. Anim Behav 32:1236–1252

Taborsky M (1985) Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. Behaviour 95:45–75

Timms AM, Keenleyside MHA (1975) The reproductive behaviour of *Aequidens paraguayensis* (Pisces, Cichlidae). Z Tierpsychol 39:8–23

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, Oxford, NY

Tomasello M, Call J, Hare B (1998) Five primate species follow the gaze of conspecifics. Anim Behav 55:1063–1069

Visalberghi E, Fragaszy DM, Savage-Rumbaugh S (1995) Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). J Comp Psychol 108:15–22

Vivien L (1973) Contribution à la connaissance de l'ethologie alimentaire de l'ichthyofaune de platier interne des recifs coralliens de Tulear. Tethys [Suppl] 5:221–308

Voelkl B, Huber L (2000) True imitation in marmosets. Anim Behav 60:195–202

Warner RR (1988) Traditionality of mating site preferences in a coral reef fish. Nature 335:719–721

Warner RR (1990) Resource assessment versus traditionality in mating site determination. Am Nat 135:205–217

Whiten A, Custance DM, Gomez J-C, Teixidor P, Bard KA (1996) Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). J Comp Psychol 110:3–14

Wickler W (1965) Die Evolution von Mustern der Zeichnung und des Verhaltens. Naturwissenschaften 52:335–341

Wickler W (1969) Zur Soziologie des Brabantbuntbarsches, *Tropheus moorei* (Pisces, Cichlidae). Z Tierpsychol 26:967–987

Wilson EO (1973) On the queerness of social evolution. Soc Res 40:144–152

Wirtz P (1996) Werkzeuggebrauch bei Lippfischen. Aquar Terr Z 1:4–5

Zahavi A (1995) Altruism as a handicap – the limitations of kin selection and reciprocity. J Avian Biol 26:1–3