3-2012

Tool Use in Fishes

Culum Brown

Macquarie University

Recommended Citation

Brown, C. (2012). Tool use in fishes. Fish and Fisheries, 13(1), 105-115.

Tool Use in Fishes

Culum Brown
Macquarie University

KEYWORDS

birds, cognition, fishes, primates, tool use

ABSTRACT

Tool use was once considered the sole domain of humans. Over the last 40 years, however, it has become apparent that tool use may be widespread across the animal kingdom. Pioneering studies in primates have shaped the way we think about tool use in animals, but have also lead to a bias both in terms of our expectations about which animals should be capable of using tools and the working definition of tool use. Here I briefly examine tool use in terrestrial animals and consider the constraints of the current working definition of tool use in fishes. Fishes lack grasping limbs and operate underwater where there are clear constraints with respect to the physics of tool use that differ dramatically from the terrestrial environment. I then examine all of the documented accounts of tool use in fishes. The review reveals that tool use seems to be confined to a limited number of fish taxa, particularly the wrasse, which may show similarities with the greater than expected number of examples of tool use in primates and corvids amongst mammals and birds, respectively. As fish are seldom studied as intensely as birds and mammals, there is a clear need for further observation of tool use in fishes. It is likely that further examples will be unveiled allowing us to perform comparative analyses of the evolution of tool use in fish.

Introduction

Tool use in the Hominidae is often hailed by anthropologists as the defining moment in the evolutionary history of humans as a clear sign of the emergence of intelligence some 2.5 Ma (Ambrose 2001). Not so long ago, tool use was thought to be a unique human trait, but researchers were quick to turn to primates in a bid to find an evolutionary precursor. Sure enough there are now numerous accounts of tool use in primates including using sticks to fish for termites and using a hammer and anvil to crack open nuts (Seed and Byrne 2010). More controversially, there are accounts of macaques, *Macaca fuscata* (Cercopithecidae), using water as a tool whereby they pickup handfuls of wheat and grit and toss them into the water (Kawai 1965). The wheat floats and the grit sinks enabling them to eat the wheat without ingesting a mouthful of dirt. Similarly, orangutans, *Pongo abelii* (Hominidae), collected mouthfuls of water and spat it into transparent tubes to access peanuts floating inside (Mendes et al. 2007). Reader and Laland (2002) showed that tool use in primates is correlated with neocortex and striatum size and thus is arguably a cognitively demanding exercise. The discovery of tool use in birds, however, clearly shows that tool use has arisen multiple times throughout evolutionary history as birds split from their reptile ancestors 150 Ma. Thus, tool use, far from being a human-specific trait, may in fact be more common amongst animals than previously thought.

Accounts of tool use in birds are perhaps equally common as those in primates. Analysis of tool use in birds suggests that tool use has emerged independently multiple times and, like primates, is correlated with relative size of various brain lobes (Lefebvre et al. 2002). The most celebrated example is that of New Caledonian crows, *Corvus moneduloides* (Corvidae), that use tools fashioned from pandanas leaves to extract insects from difficult to reach crevices (Hunt 1996). Egyptian vultures, *Neophron percnopterus* (Accipitridae), drop rocks on ostrich, *Struthio camelus* (Struthionidae), eggs to break them open (van Lawick-Goodall and van Lawick-Goodall 1966). A less complex form of tool use (proto tool use) is also displayed by corvids on the shoreline of the Firth of Forth, Edinburgh, where shellfish are collected at low tide and dropped onto the cyclepath to break them open (personal observations). Calculations have shown that the crows drop the shells from a specific height (5 m) to ensure the break open with minimal energetic expenditure wasted on repeated dropping attempts (Zach 1979). Male palm cockatoos, *Probosciger aterrimus* (Cacatuidae), wield a stick which they use to beat on hollow tree trunks as part of their mating display (Wood 1984). Thus, both primates and birds display tool use across three principal categories of food extraction, food capture and agonism and within these taxa there are clear parallels between tool use in corvids and primates where tool use seems to be particularly prevalent (Bentley-Condit and Smith 2009).

Tool use has also been documented in insects (see Pierce 1986 for a review) and other invertebrates, the most celebrated of which occurs in octopus. Veined octopus, *Amphioctopus marginatus* (Octipodidae), carries around coconut shells whilst moving across soft sediment where little cover is available. They can employ the shell as a shelter when threatened. The behaviour is unusual because the octopus obviously bare a significant cost when the shell is not in use and must employ an unusual form of locomotion (stilt walking) to compensate for their cumbersome baggage (Finn et al. 2009). Other forms of tool use in invertebrates include the use of leaves or sand pellets to transport food to the nest in various species of ants (Fellers and Fellers 1976). Pavement ants, *Tetramorium caepitum* (Formicidae), use grains of sand as a tool when they are raiding bee nests for pollen. If a guard bee is present at the nest during the raid, the ants drop soil onto it and may kill it in the process (Schultz 1982).

These examples illustrate the diversity of tool use in the animal kingdom and lead us to question what an appropriate definition of tool use might be and whether it is really associated with cognitive complexity. There are almost as many definitions of tool use as there are primatologists (see review by Schumaker et al. 2011) but some of the most commonly cited definitions are those provided by Beck, Alcock and Goodall. Virtually, all the definitions were developed with primates in mind. Jane Goodall describes tool use as the use of an external object as a functional extension of mouth or hand in the attainment of an immediate goal (van Lawick-Goodall 1970). Alcock (1972), on the other hand, describes it as the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal’s efficiency in altering the position or form of some separate object. Whilst Beck (1980) further expanded the definition that the external employment of an unattached object to alter more efficiently the form, position or condition of another object, another organism or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool. Beck’s definition is largely considered the gold standard of tool use. The trouble with most definitions is that they are somewhat arbitrary and would not adequately account for the variety of tools humans use, let alone tool use across the animal kingdom. None of them make any mention of the requirement of enhanced cognitive ability.

Beck makes the interesting addition in that the tool must be unattached and held by the user which incorporates Boswall’s notion of ‘true’ tool use (Boswall 1983). In his examination of tool use in birds, Boswall (1983) asserted that ‘borderline’ tool use involves tools that are part of the substrate. Thus, if a baboon, *Papio paio* (Cercopithecidae), cracks a nut by bounding against a rock it is borderline tool use, but if the baboon cracks a nut by striking it with a rock it counts as true tool use. Most people would see in this example the difficulty in applying stringent rules about whether the tool is attached or otherwise. Others have argued against the inclusion of tool 'attachment' to the definition on the grounds that we are really concerned with the degree of control the animal exerts over the tool (e.g. St. Amant and Horton 2008). If the animal can indeed control the tool even if it is attached to the ground, then this should still count as tool use. This would account for at least some of the ambiguities of applying Beck's definition and indeed he later redefined tool use to include those situations where the animal exerted control over the tool even if it was attached to the substrate (Schumaker et al. 2011).

Beck (1980) himself argued that the definition of tool use does not necessarily reflect on the cognitive complexity of the task. This is striking because researchers often assume that tool use is cognitively demanding (see Lefebvre et al. 2002 and Reader and Laland 2002 for evidence that it might be) and this assumption has limited the number of taxa that we expect tool use to occur. It is quite likely that many of the behaviours involving tools performed by invertebrates, for example, are completely genetically controlled and require no cognitive processing whatsoever. Thus, one must ask why we are interested in studying tool use in the first place and how do we explain tool use in cases that are clearly not linked with cognition?

For the most part, students of anthropology and primatology have been fervently arguing that tool use is intimately related to the evolution of cognition in humans. But by focussing solely on tool use in humans and their allies (and by tweaking the definition to ensure tool use remains their sole domain), we are likely to miss a broader evolutionary picture. If we are truly interested in the biological significance of tool use, then one might also consider tool use within a much broader framework which may include other complex environmental manipulations such as nest building (Hansell and Ruxton 2008). This perspective, however, has been largely ignored perhaps because nest building is extremely widespread across the animal kingdom and thus not unique enough to warrant special attention. This is somewhat surprising considering Beck himself points out that there is very little difference between tool use and building nests. Currently, anything that is constructed but not carried (such as a nest) would be excluded from most forms of the definition of tool use, thus nests and other constructions have long been left out of any analysis of tool use. It may be, however, that tool use has its origins in the manipulation of other environmental elements, for example in the production of a nest.

Perhaps the most important element of tool use from a cognitive perspective is the intention of the user whilst using the tool. It is quite clear in the example above that the baboon means to access the nut inside the shell and lacks the physical capability to do it unless a tool is sort to aid in the extraction process. Whether the animal breaks the nut against a rock by holding the nut or the rock seems to make little difference so long as the goal is achieved. Such trivialities act as a smoke-screen that distracts us from our true purpose of identifying the biological significance of tool use. Rather than making the definition more complicated by demanding that a tool be employed in a specific manner, as Alcock, Beck and Boswall propose, I suggest Goodall had it right from the beginning when she was less concerned about how the feat is achieved and focussed on identifying the animal's immediate goal. Thus, a tool may be recruited to achieve a goal when the animal lacks a morphological or behavioural adaptation suitable for dealing with the problem. This is particularly important when dealing with animals lack grasping appendages, such as ungulates or fishes, where carrying a tool is exceedingly unlikely but they may, nevertheless, manipulate fixed items such as anvils to achieve a goal. Note also that this definition would not exclude nest building and would facilitate a broader approach to identifying the evolutionary origins of tool use as advocated by Hansell and Ruxton (2008). In these instances, a broader perspective is clearly required focussing on the degree to which the tool is manipulated and the intent of the user.

Whilst the cognitive tool user hypothesis has totally dominated research on the topic for over three decades, it has done so at the expense of other equally plausible hypotheses. For example, it may also be the case that tool use only exists in those species that are not limited by some anatomical constraint (such as a lack of grasping limbs). Alternatively, one might take a more ecological approach and propose that tool use only occurs in those environments where tools are readily available (i.e. ecological constraint). Both of these hypotheses may be completely independent of cognition, or there may be interesting interactions between all three hypotheses. In any case, all three provide very different starting points for our search for evidence of tool use in the animal world.

In the case of fishes, one might expect to see different taxa using tools depending on the hypothesis we are testing. In the case of the cognitive hypothesis, one would expect that tool use would be associated with a relatively large brain. The ecological constraint hypothesis would suggest that benthic fish are more likely to be tool uses, simply because there is no structure in the pelagic realm to manipulate other than water itself. Lastly, if we take a broader approach as suggested by Hansell and Ruxton (2008), we might expect fish that regularly engage and manipulate objects in their environment (perhaps to build a nest or in search of prey) will be more likely to engage in tool use. If all three factors are additive in some way, we might expect that large brained, benthic species that regularly manipulate objects in their environments to be most likely to engage in tool use.

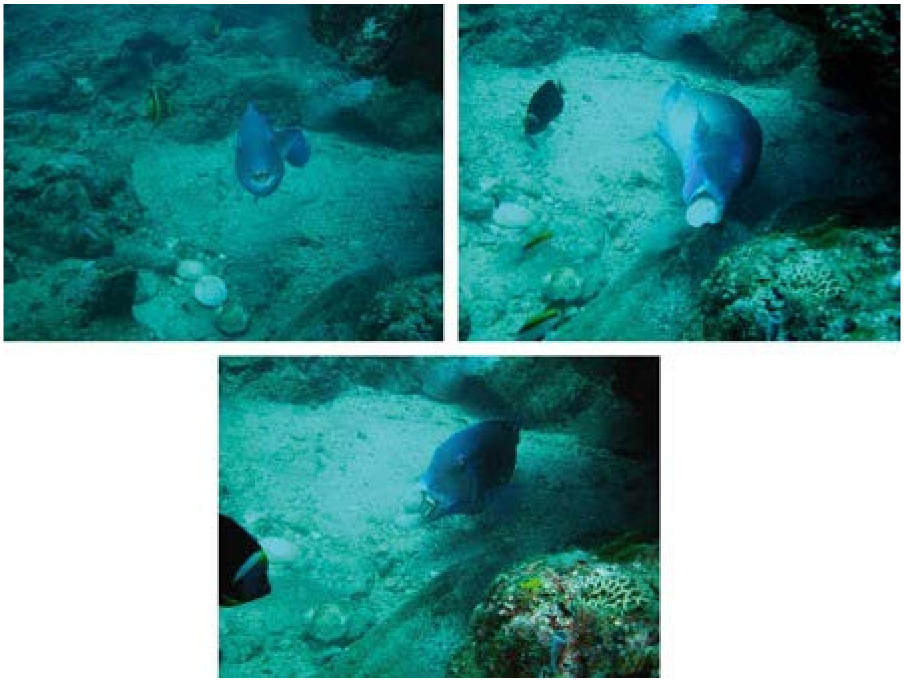
Tool use in fishes

Despite the fact that fish are not renowned for their intelligence, there is an increasing body of evidence that suggests that they have been largely underestimated in terms of the cognitive ability (Brown et al. 2011). Most of the phenomena of interest to primatologists can also be found in fishes including examples of social intelligence, culture and tool use (Bshary et al. 2002). Thus, fishes provide further opportunity to examine the evolution of a number of cognitive traits including tool use. Fishes also provide an opportunity to re-examine the tool use in a much broader group of animals and subsequently allow us to reflect on the definition of tool use and its evolutionary origins in a group of animals far removed from primates. The standard definition of tool use is largely inadequate for fishes for two reasons: (i) fish lack grasping appendages, so the only way they can use a ‘true tool’ is if they hold it in their mouth (anatomical constraint) and (ii) fish live in water where the physics of using tools are completely different to those operating in air (ecological constraint). Water is more viscous than air and material is more buoyant in water than in air, so using a tool in the standard way may be ineffective underwater. Fish cannot drop items from great heights in the hope that they will break open on a hard substrate (sensu crows), nor can they drop rocks on prey items in the hope that they will crack open (sensu vultures). Similarly, swinging ‘hammers’ through the water is equally difficult and ineffective. In all cases, the items weigh too little or fall too slowly to have any impact. Moreover, if a tool is held in the mouth to access a prey item, then it must be disposed of very quickly to ingest the prey item. In a highly competitive environment where scroungers abound, this is not likely to be a successful strategy; far better to maintain procession of the prey (see also an example of this constraint in birds; Morand-Ferron et al. 2004). Both of these factors place considerable constraints on tool use in fishes. Thus, tool use in fishes requires a less primate-centric definition that takes these factors into account. Thus, a suitable definition of tool use in fish might be ‘the active manipulation of an external object in the attainment of a goal’ sensu Goodall.

In reviews of tool use, fishes are frequently excluded (e.g. Bentley-Condit and Smith 2009). Fishes are overlooked for a number of reasons including the fact that there is a low expectation amongst cognitive scientists and comparative psychologists that fish are smart enough to use tools, and, secondly, fish are seldom observed with the same level of scrutiny afforded to primates and birds. Observing fish in their natural environment is inherently difficult, thus it is likely the examples of tool use in fish remain undisclosed. Despite these difficulties, however, there have been some examples of fish using tools in the literature and, interestingly, there are parallels with primates and birds in that tool use seems to be confined to a few families.

Although some would include the manipulation of conspecifics (or even heterospecifics) in their definition of tool use (e.g. social tool use; Bard 1990), here I refine my discussion to more widely accepted examples. For a discussion on manipulation of conspecifics in fishes see Bshary (2006). I have also excluded nest building because it is an extremely common behaviour in fishes with at least a third of the 30+ thousand species of fish known to build a nest of some sort (Bshary et al. 2002). It would be a massive undertaking in its own right to compile a database of nest building in fishes and compare it with the emerging evidence of tool use.

Figure 1. A tuskfish picks up a bivalve and repeatedly smashes it against anvil. Notice the blows are aimed specifically at the pointed section of the anvil to achieve maximum effect. Numerous scroungers are evident in the foreground and background (Jones et al. 2011).

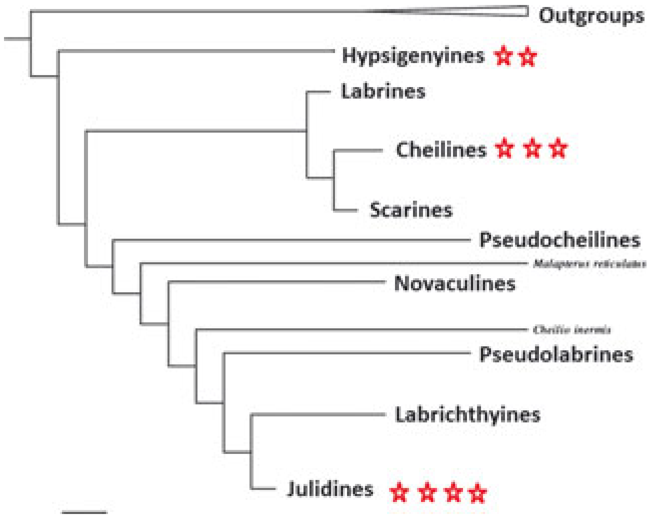


Anvil use in fishes

Jones et al. (2011) showed graphic photos of a black-spotted tuskfish, *Choerodon schoenleinii* (Labridae), cracking open a bivalve on an anvil. In this case the fish grasps the bivalve in its formidable jaws and takes it to a feeding station that is equipped with appropriate anvils embedded in the substrate. The fish delivers alternate, well-placed blows to the left and right by rapidly rotating its body, eventually breaking open the shell. The collection of shells scattered around the feeding station suggests that this is a common occupation for this fish; moreover, similar collections of broken shells (middens) can be observed accords the Great Barrier Reef, suggesting the behaviour is widespread (Fig. 1). The sister species, *Choerodon anchorago*, takes a very similar approach but tends release the shellfish at the last second effectively throwing the shell a very small distance before it hits the anvil (Bernardi 2011). The yellow-headed wrasse, *Halichoeres garnoti* (Labridae), also conducts this behaviour to open scallops (Coyer 1995). Other species of wrasse (*Coris angulata*, *Cheilinus fasciatus*, *Cheilinus lunulatus*; Labridae) have been reported to crush sea urchins against corals and rocks to break off the spines, spilt the test and access the soft body parts inside (Fricke 1971; Wirtz 1996). These wrasse also have preferred feeding stations where they bring the urchin for processing (Fricke 1971). Observations of this kind have been made both in the wild and in captivity in a number of Thalassoma species (Heiser 1981; Pas´ko 2010). In the case of the broom wrasse, *Thalassoma Hardwicke* (Labridae), for example, the fish was held in captivity in a communal aquarium and fed large pellets. The pellets were too big for the fish to ingest so it used an anvil to smash food into more manageable pieces (Paśko 2010). Once again the fish had a preferred location in the tank where the pellets were taken for processing.

All of these examples show a common thread of collecting the prey item, delivering it to a feeding station and smashing the prey open on preferred anvils. Interestingly, they come from a single marine fish family, the Labridae, consisting of 600 species in 82 genera. If one examines where the species that have been observed using anvils to break open prey items are located in the wrasse phylogeny, it is apparent that this behaviour is either ubiquitous or it has emerged independently in three of the nine tribes (Fig. 2). There have been four accounts in the Julidines, three in the Cheilines and two in the Hypsigenuines covering the entire phylogenetic breadth of the family and some 50 Myr of evolution. Currently, the most parsimonious explanation is that the behaviour has evolved independently multiple times in the wrasse, but it is highly likely that further observation of these fish in the wild will reveal other examples of this behavior and thus the account may change.

Figure 2. Phylogeny based on mitochondrial and nuclear markers of the wrasse fishes showing the nine tribes (based on Cowman et al. 2009). Stars refer to the number of reports of tool use in the tribe.



True tool use

According to the definition of tool use adopted by Beck (1980), the examples of anvil use would not be included in a checklist of tool use and would be filed under ‘border line tool use’ as defined by Boswall (1983) because the tool is attached to the substrate and not carried by the fish. Nevertheless, the intention of the fish is very clear and these series of actions would easily be accommodated in Goodall’s definition. For the hard-core tool use lovers, however, there are other examples of tool use in fish that would satisfy even Beck's definition. A number of fish species lay their eggs on various substrates which are more or less movable in an emergency. In the South American cichlids (Cichlidae), for example, eggs may be glued to leaves or small rocks which can then be used as 'tablets' to transport the eggs around the territory (Timms and Keenleyside 1975; Keenleyside 1979). In the banded acara, *Aequidens paraguayensis*, the parents apparently test various leaves prior to selecting them to ensure they are easy to move (Keenleyside and Prince 1976). Similarly, the brown hoplo catfish, *Hoplosternum thoracatum* (Callichthyidae), lays its eggs on leaves and may transport them back to the nest if the leaves become detached (Armbrust 1958).

It is easy to imagine how the use of tablets to move eggs around evolved in cichlids and it has seemingly little to do with the evolution of 'higher' intelligence. Attaching eggs to the substrate or a nest is very common in many species of fish, especially those that display some form of parental care. Cichlids frequently attach their eggs to the underside of rocks or within a nest and will defend their nests with great vigour. If, however, the threat is too great, the parents will abandon the nest and start again. If by chance the eggs are laid on relatively small, light, detached substrata (such as leaves or small rocks), however, then the parents can pickup the 'tablet' and escape with the eggs intact. Picking up objects is a natural part of cichlid foraging behaviour and many of the cichlids also excavate the nest site by removing objects with their mouths. Thus, it is simple to see how these behaviours can be run together in a sequence that culminates in tool use. Few would argue that this behaviour emerged as the result of the evolution of enhanced cognitive capacity, but it does seem highly compatible with the notion that tool use may be associated with nest building behavior (Hansell and Ruxton 2008).

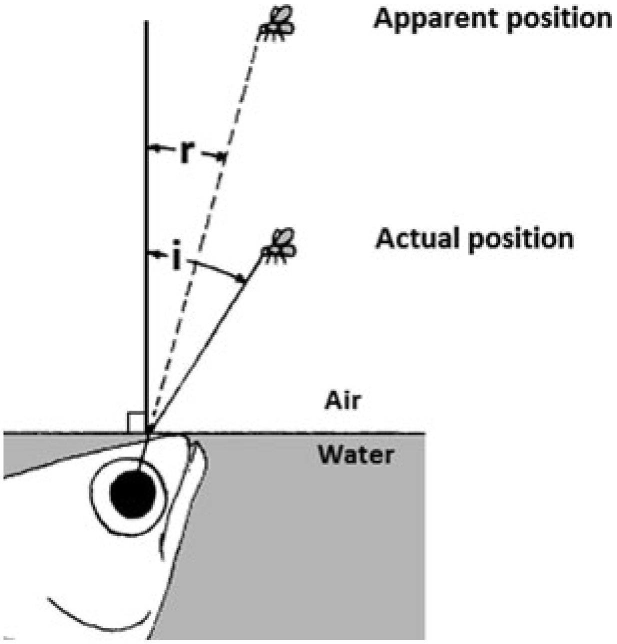
In the marine environment, similar observations of tool use have been made in association with nest site preparation in whitetail majors, *Stegastes leucoris* (Pomacentridae). When preparing the nest site, the fish ensure that the substrate is thoroughly cleaned. As part of this process, they pickup mouths full of sand and repeatedly spit it at the nest location. This form of sand blasting is apparently an effective way of removing detritus, so the eggs can be attached via adhesive strands and will not be dislodged by turbulence (Keenleyside 1979). It is unclear if this behaviour is stereotyped or if it is moderated relative to the cleanliness of the substrate. If the former then, once again, the tool use is certainly devoid of any inherent cognitive processing and again favours the nest building origins of tool use.

Water as a tool

There is some debate about whether the manipulation of water counts as tool use, although it is frequently referred to in the primate literature. If one assumes that water counts as an external agent or object, then it likely falls into the category of tool use according to most definitions. How one would begin to deal with this using Boswall's definition is far from clear as, in the case of fishes, they are immersed in the water which is clearly 'attached to the substrate'. However, if a human used a hose to clean a path, I suspect most people would agree that it falls into the common definition of tool use. So if the animal could demonstrate some sort of control over the water and use it effectively to achieve a goal, then it may count as true tool use. There are a number of documented examples of tool use associated with water in primates, a few of which are illustrated above, and researchers are quick to accept this as tool use in primates. Once we accept this position, then there seems to be little grounds for not accepting similar behaviour in fishes particularly in those instances where the intent of the animal is quite clear and there appears to be evidence that the behaviour is cognitively demanding.

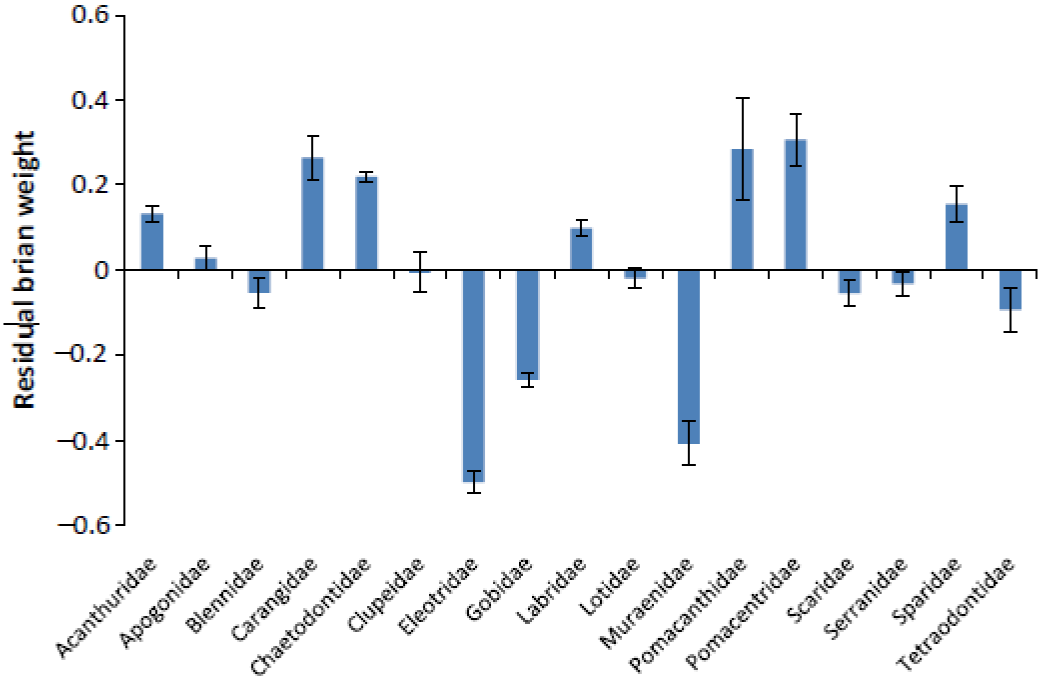
Archerfish (Toxotidae) are the ultimate archers. They squirt water from their mouths by forming a tube between their tongue and pallet to dislodge terrestrial prey items above the surface (Dill 1977). The banded archer fish, *Toxotes jaculatrix*, and the seven-spot archer fish, *Toxotes chatareus*, are both known to perform this behaviour, but much of the research has focussed on the former. What is so intriguing about this is that the squirt of water seems to be perfectly aligned with the force required to dislodge insects (Schlegel et al. 2006). Moreover, it is apparent that many aspects of the archerfish's behaviour are learnt as a result of experience. For example, archer fish have to learn to adjust the angle of their squirt to match the bending of light at the air/water interface (Fig. 3) and can determine the absolute size of their prey (Schuster et al. 2004). They also learn to adjust their targeting skills to hit moving objects (Schuster et al. 2006). For archerfish living in estuarine environments or in a habitat where the water changes temperature, the spitting angle needs to be adjusted as a function of the salinity and temperature using Snell's Law. Freshwater at 30 °C has a refraction index of 1.329, but at 10 °C this increases to 1.331. Similarly, the change from freshwater to sea water adds 0.007 to the refraction index. Thus, hitting insects in the riparian vegetation from below the water surface using a spurt of water seems to have all the hallmarks of tool use and is probably cognitively demanding.

Figure 3. Archer fish learn to adjust the angle of their spout of water when aiming at insect above the water surface using Snell's Law (after Dill 1977). According to Snell's law sin i/sin *r* = 1.330 in freshwater at 20 °C, where *r* = angle of refraction and *i* = angle of incidence.



Perhaps less well known are examples of using water as a tool can be found amongst the gouramis, wrasse and elasmobranchs. A number of species of gourami (*Trichogaster chuna*, *T. fasciata*, *T. lalius* and *T. trichopterus*; Osphronemidae) shoot jets of water above the surface of the water, a behaviour that seems to serve multiple functions in a variety of contexts (Hall 1966; Kramer 1973; Miller and Jearld 1982). In a foraging context, fish adjust their jetting behaviour to target various prey items, including flake food stuck to the side of aquaria, in a manner similar to archerfish. This behaviour was labelled 'prey-spitting' by Vierker (1975). In the nesting context the males send a jet of water through the foam nest which can have the effect of dislodging some of the eggs embedded in the foam matrix and causing them to stick to objects above the water surface. Wimmer (1970) observed that of the 123 cases where eggs were displaced in this manner, 77% of them hatched. Thus, one could speculate that the behaviour may reduce predation on the developing eggs by placing them out of harm's way in low hanging vegetation above the water surface. Alternatively, the jetting behavior may enable the male to retrieve eggs that are too highly placed in the foam nest matrix (Vierker 1975). Once again, this behaviour is intimately related to nest building and maintenance and does not appear to be cognitively demanding.

Figure 4. The relative brain weight of fish from 17 families. Positive scores represent brains that are heavier than expected for a given fish weight, whilst the opposite is true for negative scores.

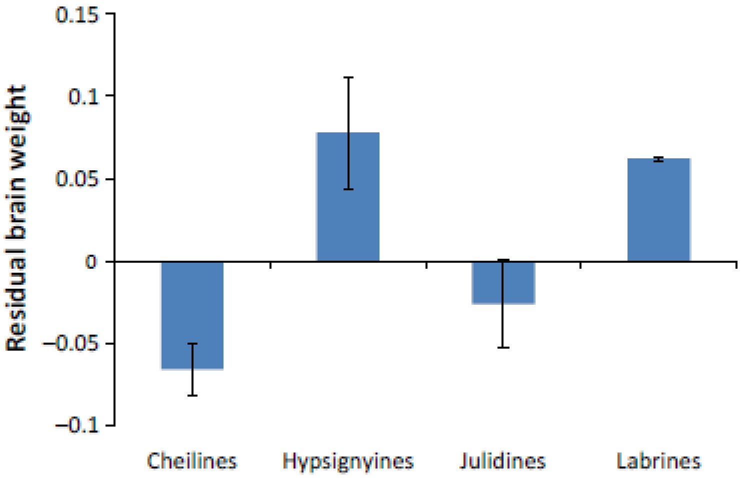


A number of species display jetting behavior below the surface of the water. The trigger fish *Pseudobalistes fuscus* (Balistidae), for example, blow water streams to turn sea urchins over to access their more vulnerable side (Fricke 1975). Similar accounts of blowing water to uncover prey have been made in various species of sharks and rays (Hueter et al. 2004). Adult fresh water stingrays, *Potamotrygon castexi* (Potamotrygonidae), used jets of water to extract food items from inside a plastic tube as part of a problem-solving strategy (Kuba et al. 2010). The finding of tool use in elasmobranchs once again suggests that tool use has arisen multiple times in fishes as elasmobranchs split from bony fish in the early Devonian. I would be willing to bet, however, that the use of water jets to dislodge prey items is ubiquitous in benthic foraging fishes and is worthy of further investigation.

Fish brains and tool use

In both birds and primates there is evidence to suggest that tool use is associated with the relative size of various brain regions (Lefebvre et al. 2002; Reader and Laland 2002). One immediately wonders if such a relationship might also exist in fish. There is an enormous amount of diversity in fish brains with respect to form and function. Some of this diversity is related to the ecology of the animals in question (Kotrschal et al. 1998). In a comparative analysis of Tanganyikan cichlids, for example, brain size was shown to vary as a function of ecological and social factors. Females that are the sole providers of their young have larger brains than those that exhibit biparental care, whereas care type did not correlate with brain size in males (Gonzalez-Voyer et al. 2009). Similar studies have shown that piscivores have larger olfactory bulbs and optic tecta than insectivores and zooplanktivores (Huber et al. 1997). Geiger (1956) suggests that trigger fish have large telencephalon relative to other fishes and members of this family are highly represented in accounts of tool use in fishes. Similarly, stingrays have the largest brains amongst the elasmobranchs (New 2001), and these species are also represented in the list of fishy tool users. It is perhaps too early to conduct similar studies with respect to tool use but there are some tantalizing suggestions that such a study would be fruitful. Given the massive diversity amongst the 600 or so species of wrasse and the fact that much is already known about their diet and phylogenetic relationships (Cowman et al. 2009), this group of fish offer a fantastic opportunity to study the relationship between tool use and brain size. If tool use is indeed cognitively demanding, then one would expect those species that are known to exhibit tool use to have larger brains than those that do not.

Figure 5. Relative brain weight of four tribes within the wrasse family.



The current limiting factor in any attempt to address this question is not the lack of information of brain size in fishes, but rather the limited observations of tool use. Nevertheless, in a preliminary attempt to show what might be possible with such data, I extracted data on brain size for teleost fish from the online database fishbase.org. The dataset refers to over 800 individuals from 340 different species. I only included data for the 17 families that had more than five species represented. I took the log of the fish weight and log of the brain weight, ran a regression and extracted the residuals. Where multiple individuals were present in the database, I calculated the mean fish and brain weights.

The analysis reveals a few interesting patterns (Fig. 4). Firstly, there are four families that seem to have unusually large brains: the Carangidae (travelley), Cheatdodontidae (butterfly fish), Pomacanthidae (angelfish) and Pomacentridae (damselfish). Virtually, all of these species are reef associated but there are essentially no reports of tool use in any of these species (except for sand blasting in damselfish). The next group comprise the Acanthuridae (surgeonfish), Labridae (wrasse) and the Sparidae (bream) all of which still have significantly larger brains than expected for their given body weight. All species belonging to the former two families are from reef habitats but the latter is conspicuous by way of the fact that it contains species living in a wide variety of environments. The wrasse are the only family of the group in which there are accounts of tool use, but it is comforting to know that they do have relatively large brains as one would expect from the cognition hypothesis.

One can also look for patterns within families. To do this I isolated the data for the wrasse, reran the regression and extracted family-specific residuals. There are limited brain data with only four of the nine tribes represented. Nevertheless, there are significant differences between tribes (Fig. 5). The Hypsigenuines and Labrines have significantly Larger brains than expected whilst the Julidines and Cheilines have significantly smaller brains than expected. This seems to bear no resemblance to the accounts of tool use in these tribes (Fig. 2). However, as I mentioned from the outset, there are very few accounts of tool use in fishes at present, there are scant data for brain weight in fishes and the measure of relative brain weight is probably not the most appropriate brain measure to employ. Nevertheless, I strongly encourage further work in this area.

Conclusions

The study of tool use in animals has been highly restricted to primates and birds and the most widely accepted definition of tool use is heavily primate centric. With a small change in the requirement that a tool must be held to be employed, we release fish from an obvious anatomical constraint. Moreover, fish also face ecological constraints because the physics of tool use in the underwater environment is vastly different to that in terrestrial environments. With these factors in mind, we can take a new look at the evolution of tool use in the largest vertebrate taxon on earth. To move forward we clearly require far more observations of tool use in fishes and then we can begin to search for ecological or morphological correlates such as relative optic tectum size and conduct phylogenetic comparative analyses. We have an expectation that benthic species that commonly manipulate their environment whilst foraging or building nests might be the mostly likely targets for tool use evolution. It seems very likely, however, that the emergence of tool use has occurred multiple times throughout evolutionary history and only a small proportion of these accounts appear to be correlated with the emergence of higher cognition. There are likely alternative reasons for the rise of the examples of tool use which are not associated with cognition, for example they have their roots in nest building or foraging behaviour. Thus, a full investigation of alternative hypotheses is required.

Acknowledgements

Culum is funded by an ARC Australian Research Fellowship. Thanks to Scott Gardner for his inspirational pictures of tusk fish using tools and Alison Jones for bringing this example to my attention.

References

Alcock, J. (1972) The evolution of the use of tools by feeding animals. Evolution 26, 464–473.

Ambrose, S.H. (2001) Paleolithic technology and human evolution. Science 291, 1748–1753.

Armbrust, W. (1958) Haltung und zucht von *Hoplosternum thoracatum. Die Aquarien und Terrarienzeitschrift* 11, 97–100.

Bard, K.A. (1990) Social tool use by free-ranging orangutans: a piagetian and developmental perspective on the manipulation of an animate object. In: *Language and Intelligence in Monkeys and Apes. Comparative Developmental Perspectives* (eds S.T. Parker and K.R. Gibson). Cambridge University Press, Cambridge, pp. 356–378.

Beck, B.B. (1980) *Tool Use in Animals*. Garland STPM Publishers, New York.

Bentley-Condit, V.K. and Smith, E.O. (2009) Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* 147, 185–221.

Bernardi, G. (2011) The use of tools by wrasses (Labridae). *Coral Reefs*, doi: 10.1007/s00338-011-0823-6.

Boswall, J. (1983) Tool use and related behaviour in birds: yet more notes. *Aviculture Magazine* 89, 170–181.

Brown, C., Laland, K. and Krause, J. (2011) *Fish Cognition and Behaviour 2e*. Wiley-Blackwell, Cambridge.

Bshary, R. (2006) Machiavellian intelligence in fishes. In: *Fish Cognition and Behavior* (eds C. Brown, K. Laland and J. Krause). Blackwell Scientific, Oxford, pp. 223–242.

Bshary, R., Wickler, W. and Fricke, H. (2002) Fish cognition: a primate’s eye view. *Animal Cognition* 5, 1–13.

Cowman, P.F., Bellwood, D.R. and van Herwerden, L. (2009) Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Molecular Phylogenetics and Evolution* 52, 621–631.

Coyer, J. (1995) Use of a rock as an anvil for breaking scallops by the yellowhead wrasse, *Halichoeres garnoti* (Labridae). *Bulletin of Marine Science* 57, 548–549.

Dill, L.M. (1977) Refraction and the spitting behavior of the archerfish (*Toxotes chatareus*). *Behavioral Ecology and Sociobiology* 2, 169–184.

Fellers, J.H. and Fellers, G.M. (1976) Tool use in a social insect and its implications for competitive interactions. *Science* 192, 70–72.

Finn, J.K., Tregenza, T. and Norman, M.D. (2009) Defensive tool use in a coconut-carrying octopus. *Current Biology* 19, R1069–R1070.

Fricke, H. (1971) Fische als Feinde tropischer Seeigel. *Marine Biology* 9, 328–338.

Fricke, H. (1975) Lo¨sen einfacher Probleme bei einem. Fisch. *Zeitschrift für Tierpsychologie* 38, 18–33.

Geiger, W. (1956) Quantitative untersuchungen über das gehirn der knochenfische, mit besonderer beru¨ cksichtigung seines relative wachstums, *I. Acta Anatomica* 26, 121–163.

Gonzalez-Voyer, A., Winberg, S. and Kolm, N. (2009) Social fishes and single mothers: brain evolution in African cichlids. *Proceedings of the Royal Society B, Biological Sciences* 276, 161–167.

Hall, D.D. (1966) Reproductive color changes in the pearl gourami, *Trichogaster leeri* (Bleeker). *Bios* 37, 104–107.

Hansell, M. and Ruxton, G.D. (2008) Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution* 23, 73–78.

Heiser, J.B. (1981) *Review of the Labrid Genus Thalassoma (Picses: Teleostei).* PhD Dissertation, Cornell University, Ithaca, NY, USA, 280 pp.

Huber, R., Van Staaden, M.J., Kaufman, L.S. and Liem, K.F. (1997) Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. *Brain, Behavior and Evolution* 5B, 167–182.

Hueter, R.E., Mann, D.A., Maruska, K.P., Sisneros, J.A. and Demski, L.S. (2004) Sensory biology of elasmobranchs. In: *Biology of Sharks and Their Relatives* (eds J.C. Carrier, J.A. Musick and M.R. Heithaus). CRC Press, Boca Raton, pp. 325–368.

Hunt, G.R. (1996) Manufacture and use of hook-tools by New Caledonian Crows. *Nature* 379, 249–251.

Jones, A., Brown, C. and Gardener, S. (2011) Tool use in the spotted tuskfish, *Choerodon schoenleinii*. *Coral Reefs* 30, 865.

Kawai, M. (1965) Newly acquired pre-cultural behavior of a natural troop of Japanese monkeys on Koshima Island. *Primates* 6, 1–30.

Keenleyside, M.H.A. (1979) *Diversity and Adaptation in Fish Behaviour*. Springer-Verlag, Berlin.

Keenleyside, M.H.A. and Prince, C. (1976) Spawning-site selection in relation to parental care of eggs in *Aequidens paraguayensis* (Pisces: Cichlidae). *Canadian Journal of Zoology* 54, 2135–2139.

Kotrschal, K., Van Staaden, M. and Huber, R. (1998) Fish brains: evolution and environmental relationships. *Reviews in Fish Biology and Fisheries* 8, 373–408.

Kramer, D.L. (1973) Parental behaviour in the blue gourami *Trichogaster trichopterus* (Pisces, Belontiidae) and its induction during exposure to varying numbers of conspecific eggs. *Behaviour* 47, 14–32.

Kuba, M., Byrne, R. and Burghardt, G. (2010) A new method for studying problem solving and tool use in stingrays (*Potamotrygon castexi*). *Animal Cognition* 3, 507–513.

van Lawick-Goodall, J. (1970) Tool-using primates and other verebrates. In: *Advances in the Study of Behavior Vol 3* (Eds D. Lehrman, R. Hinde and E. Shaw). Academic Press, New York, pp. 195–249.

van Lawick-Goodall, J. and van Lawick-Goodall, H. (1966) Use of Tools by the Egyptian Vulture, *Neophron percnopterus*. Nature 212, 1468–1469.

Lefebvre, L., Nicolakakis, N. and Boire, D. (2002) Tools and brains in birds. *Behaviour* 139, 939–973.

Mendes, N., Hanus, D. and Call, J. (2007) Raising the level: orangutans use water as a tool. *Biology Letters* 3, 453–455.

Miller, R.J. and Jearld, A. (1982) Behavior and phylogeny of fishes of the genus Colisa and the family Belontiidae. *Behaviour* 83, 155–185.

Morand-Ferron, J., Lefebvre, L., Reader, S.M., Sol, D. and Elvin, S. (2004) Dunking behaviour in Carib grackles. *Animal Behaviour* 68, 1267–1274.

New, J.G. (2001) Comparative neurobiology of the elasmobranch cerebellum: theme and variation on a sensorimotor interface. *Environmental Biology of Fishes* 60, 93–108.

Paśko, Ł. (2010) Tool-like behavior in the sixbar wrasse, *Thalassoma hardwicke* (Bennett, 1830). *Zoo Biology* 29, 767–773.

Pierce Jr, J.D. (1986) A review of tool use in insects. *The Florida Entomologist* 69, 95–104.

Reader, S.M. and Laland, K.N. (2002) Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Science USA* 99, 4436–4441.

Schlegel, T., Schmid, C.J. and Schuster, S. (2006) Archerfish shots are evolutionarily matched to prey adhesion. *Current Biology* 16, R836–R837.

Schultz, G.W. (1982) Soil-dropping behavior of the pavement ant, *Tetramorium caespitum* (L.) (Hymenoptera: Formicidae) against the alkali bee (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 55, 277–282.

Schumaker, R.W., Walkup, K.R. and Beck, B.B. (2011) *Animal Tool Behaviour: The Use and Manufacture of Tools by Animals*. The John Hopkins University Press, Baltimore.

Schuster, S., Rossel, S., Schmidtmann, A., Jäger, I. and Poralla, J. (2004) Archer fish learn to compensate for complex optical distortions to determine the absolute size of their aerial prey. *Current Biology* 14, 1565–1568.

Schuster, S., Wõhl, S., Griebsch, M. and Klostermeier, I. (2006) Animal cognition: how archer fish learn to down rapidly moving targets. *Current Biology* 16, 378–383.

Seed, A. and Byrne, R. (2010) Animal tool-use. *Current biology* 20, R1032–R1039.

St. Amant, R. and Horton, T. (2008) Revisiting the definition of animal tool use. *Animal Behaviour* 75, 1199–1208.

Timms, A.M. and Keenleyside, M.H.A. (1975) The reproductive behaviour of *Aequidens paraguayensis* (Pisces: Cichlidae). *Zeitschrift für Tierpsychologie* 39, 8–23.

Vierker, J. (1975) Beitrage zur ethologie und phylogenie der familie Belontiidae (Anabantoidei, Pisces). *Zeitschrift für Tierpsychologie* 38, 163–199.

Wimmer, R.B. (1970) An Ethological Study of the Moonlight Gourami, *Trichogaster microlepis* (Gunther). PhD Thesis, Oklahoma State University, Stillwater, OK, USA.

Wirtz, P. (1996) Werkzeuggebrauch bei Lippfschen. *Aquarium Terrarium* Z 1, 4–5.

Wood, G. (1984) Tool use by the palm cockatoo *Probosciger aterrimus* during display. *Corella* 8, 94–95.

Zach, R. (1979) Shell-dropping: decision making and optimal foraging in northwestern crows. *Behaviour* 68, 106–117.