PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

rstb.royalsocietypublishing.org

Review

Cite this article: Mann J, Patterson EM. 2013 Tool use by aquatic animals. Phil Trans R Soc B 368: 20120424.
http://dx.doi.org/10.1098/rstb.2012.0424

One contribution of 15 to a Theme Issue 'Tool use as adaptation'.

Subject Areas:
behaviour, cognition, ecology, evolution

Keywords:
tool use, aquatic, benthic, foraging, specialization, cultural transmission

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Tool use by aquatic animals

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Tool-use research has focused primarily on land-based animals, with less consideration given to aquatic animals and the environmental challenges and conditions they face. Here, we review aquatic tool use and examine the contributing ecological, physiological, cognitive and social factors. Tool use among aquatic animals is rare but taxonomically diverse, occurring in fish, cephalopods, mammals, crabs, urchins and possibly gastropods. While additional research is required, the scarcity of tool use can likely be attributable to the characteristics of aquatic habitats, which are generally not conducive to tool use. Nonetheless, studying tool use by aquatic animals provides insights into the conditions that promote and inhibit tool-use behaviour across biomes. Like land-based tool users, aquatic animals tend to find tools on the substrate and use tools during foraging. However, unlike on land, tool users in water often use other animals (and their products) and water itself as a tool. Among sea otters and dolphins, the two aquatic tool users studied in greatest detail, some individuals specialize in tool use, which is vertically socially transmitted possibly because of their long dependency periods. In all, the contrasts between aquatic- and land-based tool users enlighten our understanding of the adaptive value of tool-use behaviour.

1. Introduction

Of the estimated two million extant marine animal species, only 8% have been described [1], so it is no surprise that we know very little about aquatic animal tool use. Two of the most familiar cases, sea otters (*Enhydra lutris*) and bottlenose dolphins (*Tursiops* sp.) [2–4], stand out partly because tools are brought to the surface; much less is known about tool use that takes place completely underwater. However, to fully understand the proximate and ultimate functions of tool use, we must consider tool-use behaviour in all environments, including where it might be least expected. Accordingly, we review tool-use and tool-use-like behaviour by wild animals whose primary habitat is in the water (e.g. aquatic birds are excluded).

Because most of our knowledge regarding animal tool use comes from land-based systems, care must be taken when defining tool use to ensure the definition is also appropriate for aquatic animals. In this review, we adopt the definition recently proposed by Shumaker *et al.* [5] with one modification (italicized word): the *conditional* external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool [5, p. 5]. By adding the word conditional, we emphasize that tools must be used in a specific context, 'purposively to achieve a goal' [5, p. 8]. Thus, we do not consider nests, shelters and/or objects that are perpetually worn or carried as tools unless they are manipulated in a specific way when an appropriate context arises (e.g. predator). As in the original definition, we interpret the word 'holds' liberally, because many aquatic organisms have little ability to *hold* objects, but we do maintain that an object must be directly manipulated for it to be a tool.

Studies of tool use in aquatic systems differ remarkably from those on land. In particular, observational biases play a much larger role because of the challenges associated with underwater research. This is even further exacerbated by the fact that tool use is generally a small proportion of an animal's activity budget, meaning that many hours of observation are required [6]. Furthermore, research in aquatic systems is primarily restricted to coastal, shallow and surface water habitats more than pelagic, resulting in both environmental and taxon-specific biases (e.g. aquatic mammals must surface to breathe and thus are easier to observe). Additionally, while there is long-standing interest in tool use by birds and primates [7,8], tool use in aquatic fauna has received less attention. Many potential cases of aquatic tool use are not described as such and only offer basic descriptive data. Nonetheless, tool use (or potential tool use) occurs in echinoids, crustaceans, gastropods, cephalopods, marine mammals and both ray-finned and cartilaginous fishes.

2. Aquatic tool users

In our review, we found 30 aquatic species that use tools (table 1). Additional species exhibit tool-use-like behaviour, but more observations are required to establish whether the behaviour qualifies as tool use. In table 1 and below, we summarize these behaviours according to their function.

(a) Protection

Most object manipulation by aquatic invertebrates involves barricading and/or camouflage. Numerous crab species carry or 'wear' objects such as plant debris, shells, rocks, algae, aquatic animals and/or various other objects that may provide a variety of possible benefits, including camouflage and protection from predators, the elements and/or conspecifics [11,12,16,21,22,48, 51,53–55,57]. Several urchin species and gastropods of the family Xenophoridae also decorate themselves, which may provide similar benefits [13,20,52,56,58,59]. While many of these behaviours might be tool use, most descriptions are not sufficiently detailed to determine whether the objects are used conditionally, i.e. purposively manipulated to achieve some goal. However, studies on four species of crabs and three species of urchins provide adequate data to confirm tool use (table 1).

Cephalopods also use tools for protection. Veined octopodes (*Amphioctopus marginatus*) off the coast of Northern Sulawesi and Bali in Indonesia have recently been observed using coconut shells for protection [15]. These octopodes carry shell(s) around in a non-functional form, and then use their tools when threatened by creating an enclosed dome-like shelter. This suggests both goal-directed behaviour and implementing the tool only as required. Octopodes, as well as squids and cuttlefishes, also use water as a tool for protection by using jets of water to aid in burrowing for camouflage [14,17–19].

(b) Parental care

Several fish species use water as a tool for parental care (table 1). In fact, hundreds of fish species fan their eggs with water to keep them clean and oxygenated [47], but we have difficulty considering such behaviour tool use, because there is no delineated object separate from the environmental medium. This contrasts with gouramis, which use discrete water jets as tools to place and retrieve their eggs above water [25,26].

Other fishes use objects derived from the substrate for parental care. Whitetail majors (*Stegastes leucorus*) 'sand blast' rock surface nest sites to clean them before laying eggs [24]. Several species of cichlids and at least one species of catfish lay their eggs on detached leaves or loose detritus that can be moved when the eggs are in danger or retrieved if leaves become detached from the nest [24,49,50,61]. While we consider the first case tool use, the second case is ambiguous because leaves could function primarily as substrate for egg attachment (not tool use) rather than as a mode of transportation (tool use).

(c) Foraging

Most aquatic tool use occurs in a foraging context (table 1). Many aquatic animals use water jets to locate and capture prey with two of the best-known cases occurring in archerfish [36,37], but similar behaviour also occurs in gouramis [25,38,39], pufferfish [35], triggerfish [33], rays [28,34], cephalopods [14,31] and perhaps Irrawaddy dolphins (*Orcaella brevirostris*) [62,63]. Although water jets can be viewed as 'discrete' objects, many cases of water use are less discrete and similar to some parental care behaviours (egg-fanning). Rays and skates fan water to help uncover benthic prey [46], imprints of which can even be found in the geological record [68]. Killer whales (*Orcinus orca*) create waves, sometimes singly but usually in coordinated groups, to wash prey off ice floes [45]. As with egg-fanning, we have difficulty considering these behaviours tool use, because the water being used is not easily differentiated from the environmental medium.

Other object use is less ambiguous and clearly meets the definition of tool use. For example, octopodes use objects to prop open bivalves, allowing them to eat the soft prey inside [29,30], but probably the most noted example of aquatic tool use occurs in sea otters. When foraging, sea otters often use objects as anvils to smash open prey [2], primarily gastropods and bivalves [69]. In contrast to anvil use by some fish [70], otters directly manipulate their anvils. Otters also use objects as hammers, or use one as a hammer and another as an anvil, and even sometimes wrap crabs in kelp to immobilize them while the otters consume other captured prey. Sea otters also use tools underwater by using rocks or large shells to pry or hammer abalone from the substrate [2].

In addition to water use by killer whales and Irrawaddy dolphins, cetaceans demonstrate a variety of other tool-use, or possible tool-use, behaviour. Humpback whales (*Megaptera novaeangliae*) singly and collectively expel bubbles to create nets that encircle, contain and concentrate schooling prey for easy gulping [27,71]. Bottlenose dolphins (*Tursiops truncatus*) in Florida Bay use a similar netting technique known as mud-ring feeding. One dolphin encircles prey with a mud plume by beating its tail flukes on the substrate, causing fish to jump into the mouths of one or more waiting dolphins [40]. Lone dolphins off the Florida Keys have also been observed creating mud plumes to catch prey [41].

One of best known cases of cetacean tool use involves a subset (approx. 5%) of the population of bottlenose dolphins in Shark Bay, Australia. These dolphins (the spongers) tear basket sponges up from the seabed and wear them over their beaks for protection while foraging (sponging) along the seafloor [3,4,72]. A similar behaviour has been observed once in a humpback dolphin (*Sousa chinensis*) off the northeast coast of Australia [65], but more observations are required. Sponging is thought to provide access to otherwise inaccessible prey (primarily barred sandperch, *Parapercis nebulosa*) and reduce intraspecific competition [72]. To date, over 50 spongers have

Table 1. Tool use by aquatic animals. All fish names are according to Froese & Pauly [9], while names for all other fauna are from [10]. Numbers in brackets indicate sources.

taxa	common name	behaviour	tool use	function	tool type
Dardanus arrosor[b]	striated hermit crab	carry anemones for protection from predators [11]	yes	protection	benthic: animal
Diogenes edwardsii[b]	Edward's hermit crab	carry anemones for protection from predators [12]	yes	protection	benthic: animal
Lytechinus variegatus	variegated or green sea urchin	hold objects for protection from UV light [13]	yes	protection	benthic: abiotic, algae, plant, animal
Octopus vulgaris	common octopus	squirt water jets to aid in burrowing [14]	yes	protection	benthic, mid-water, surface: water
Amphioctopus marginatas	veined octopus	use coconut shells for protection [15]	yes	protection	benthic: plant
Pagurus pollicaris[b]	grey hermit crab	carry anemones for protection from predators [16]	yes	protection	benthic: animal
Rossia pacifica	North Pacific bobtail squid	squirt water jets to aid in burrowing [17]	yes	protection	benthic, mid-water, surface: water
Sepia officinalis	common cuttlefish	squirt water jets to aid in burrowing [18]	yes	protection	benthic, mid-water, surface: water
Sepietta sp.	bobtail squids	squirt water jets to aid in burrowing [19]	yes	protection	benthic, mid-water, surface: water
Sepiola sp.	bobtail squids	squirt water jets to aid in burrowing [19]	yes	protection	benthic, mid-water, surface: water
Strongylocentrotus droebachiensis	green sea urchin	hold objects for protection from waves and UV light [20]	yes	protection	benthic: abiotic, algae, plant, animal
Tiarinia cornigera[b]	crab	carry objects for camouflage from predators [21,22]	yes	protection	benthic: algae
Tripneustes ventricosus	sea egg	hold objects for protection from UV light [23]	yes	protection	benthic: abiotic, algae, plant, animal
Stegastes leucorus	whitetail major	blast rocks with sand prior to egg attachment [24]	yes	parental care	benthic: abiotic
Trichogaster chuna	honey gourami	squirt water jets to attach and retrieve eggs [25]	yes	parental care	benthic, mid-water, surface: water
Trichogaster lalius	dwarf gourami	squirt water jets to attach and retrieve eggs [25]	yes	parental care	benthic, mid-water, surface: water
Trichogaster microlepis	moonlight gourami	squirt water jets to attach and retrieve eggs [26]	yes	parental care	benthic, mid-water, surface: water
Enhydra lutris	sea otter	immobilize prey with kelp [2]	yes	foraging	benthic, mid-water, surface: algae
Enhydra lutris	sea otter	extract prey using objects as hammers and anvils [2]	yes	foraging	benthic: abiotic, animal
Enhydra lutris	sea otter	pry and hammer prey to detach them [2]	yes	foraging	benthic: abiotic, animal
Megaptera novaeangliae	humpback whale	encircle prey with bubble nets [27,71]	yes	foraging	surface: air
Myliobatis tenuicaudatus	eagle ray	squirt water jets to uncover prey [28]	yes	foraging	benthic, mid-water, surface: water
Octopus sp.	octopodes	prop open bivalves with objects during foraging [29,30]	yes	foraging	benthic: abiotic, animal
Octopus vulgaris	common octopus	squirt water jets to aid in foraging [31]	yes	foraging	benthic, mid-water, surface: water
Potamotrygon falkneri	largespot river stingray	squirt water jets to extract food from tubes [32]	yes	foraging	benthic, mid-water, surface: water
Pseudobalistes fuscus	yellow-spotted triggerfish	squirt water jets to flip over prey [33]	yes	foraging	benthic, mid-water, surface: water
Rhinoptera bonasus	cownose ray	squirt water jets to uncover prey [34]	yes	foraging	benthic, mid-water, surface: water
Sepia officinalis	common cuttlefish	squirt water jets to uncover prey [14]	yes	foraging	benthic, mid-water, surface: water
Tetraodon lineatus	globe fish	squirt water jets to extract prey [35]	yes	foraging	benthic, mid-water, surface: water

(*Continued.*)

Table 1. (*Continued.*)

taxa	common name	behaviour	tool use	function	tool type
Toxotes chatareus	spotted archerfish	squirt water jets to stun prey [36]	yes	foraging	benthic, mid-water, surface: water
Toxotes jaculatrix	banded archerfish	squirt water jets to stun prey [37]	yes	foraging	benthic, mid-water, surface: water
Trichogaster chuna	honey gourami	squirt water jets to stun prey [25]	yes	foraging	benthic, mid-water, surface: water
Trichogaster fasciata	banded gourami	squirt water jets to stun prey [25]	yes	foraging	benthic, mid-water, surface: water
Trichogaster lalius	dwarf gourami	squirt water jets to stun prey [25]	yes	foraging	benthic, mid-water, surface: water
Trichogaster trichopterus	three spotted gourami	squirt water jets to stun prey [38,39]	yes	foraging	benthic, mid-water, surface: water
Tursiops sp.	bottlenose dolphins	wear sponges for protection during foraging [3,4]	yes	foraging	benthic: animal
Tursiops truncatus	bottlenose dolphin	encircle prey with mud plumes [40,41]	yes	foraging	benthic: abiotic
Octopus vulgaris	common octopus	squirt water jets to repel scavenging fish [42]	yes	other	benthic, mid-water, surface: water
Octopus vulgaris	common octopus	squirt water jets to move unwanted debris [14]	yes	other	benthic, mid-water, surface: water
Octopus vulgaris	common octopus	squirt water jets to deter human experimenters [43]	yes	other	benthic, mid-water, surface: water
Enhydra lutris	sea otter	use kelp to maintain buoyancy and location [44]	yes	other	benthic, mid-water, surface: algae
Pagurus pollicaris[b]	grey hermit crab	carry anemones for balance [16]	yes	other	benthic: animal
Orcinus orca	killer whale	wash prey off ice floes with waves [45]	TDD	foraging	surface: water
Superorder: Batoidea	rays and skates	fan water to uncover prey [46]	TDD	foraging	benthic, mid-water, surface: water
superfamily: Osteichthyes	bony fishes	many species fan water to care for their eggs [47]	TDD	parental care	benthic, mid-water, surface: water
family: Aethridae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Cichlidae	cichlids	some species lay eggs on mobile leaves [24,49,50]	CU, FU	unclear	benthic: plant
family: Cyclodorippidae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Diogenidae[a]	lefthanded hermit crabs	some species carry objects [12,48,51]	CU, FU	unclear	benthic: animal
family: Dorippidae	sumo crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Dromiidae	sponge crabs	all species carry objects [48]	CU, FU	unclear	benthic: animal
family: Echinidae	urchins	some species carry objects [52]	CU, FU	unclear	benthic: abiotic, algae, plant, animal
family: Echinometridae	urchins	some species carry objects [52]	CU, FU	unclear	benthic: abiotic, algae, plant, animal
family: Epialtidae	crabs	some species carry objects [53,54]	CU, FU	unclear	benthic, mid-water, surface: algae
family: Ethusidae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Hepatidae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Homolidae	carrier crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Inachidae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal

(*Continued.*)

Table 1. (*Continued.*)

taxa	common name	behaviour	tool use	function	tool type
family: Latreilliidae	longleg crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Majidae[a]	crabs	some species carry objects [48,55]	CU, FU	unclear	benthic: animal
family: Oregoniidae	crabs	some species carry objects [48]	CU, FU	unclear	benthic: animal
family: Paguridae[a]	righthanded hermit crabs	some species carry objects [12,51]	CU, FU	unclear	benthic: animal
family: Parechinidae	urchins	some species carry objects [56]	CU, FU	unclear	benthic: abiotic, algae, plant, animal
family: Pilumnidae	true crabs	some species carry objects [57]	CU, FU	unclear	benthic: abiotic
family: Urechinidae	uchins	some species carry objects [58]	CU, FU	unclear	benthic: abiotic, animal, protists
family: Xenophoridae	snails	some species carry objects [59]	CU, FU	unclear	benthic: abiotic, animal
Inia geoffrensis	Amazon river dolphin	carry and hold objects [60]	FU	unclear	benthic: abiotic, plant
Megalechis thoracata	spotted hoplo	lay eggs on mobile leaves [61]	CU, FU	unclear	benthic: plant
Orcaella brevirostris	Irrawaddy dolphin	squirt water jets during foraging [62,63]	FU	unclear	benthic, mid-water, surface: water
Sousa chinensis	Indo-Pacific humpback dolphin	throw sea shells during social play [64]	FU	unclear	benthic: animal
Sousa chinensis	Indo-Pacific humpback dolphin	carry marine sponges during foraging [65]	FU	unclear	benthic: animal
Tegula brunnea	brown tegula	moves pebbles along foot when inverted [66]	CU, FU	unclear	benthic: abiotic
Tegula funebralis	black tegula	moves pebbles along foot when inverted [66]	CU, FU	unclear	benthic: abiotic
Tursiops sp.	bottlenose dolphin	play with seagrass, possibly as practice foraging [67]	FU	unclear	benthic: plant

[a] Indicates that for most species tool use cannot be determined, but see[b], and TDD, CU and FU indicate that the tool is difficult to differentiate from the environmental medium, conditional use of the tool is unclear, and function is unclear, respectively.

been identified in each (western and eastern) gulf of Shark Bay [4,73]. Dolphins primarily use sponges of the genus *Echinodictyum*, but also *Ircinia* and *Pseudoceratina* [74], and sometimes even non-conical sponges when first learning to sponge, all of which only exist in channel habitat [72,75]. In fact, sponging does not occur in 95% of the eastern gulf that we have surveyed, but we recently identified three new spongers in several previously unexplored channels.

Shark Bay dolphins use objects in several other ways that may also prove to be tool use. Young dolphins occasionally carry and/or play with seagrass, which may be a form of 'practice foraging' [76]. Dolphins have also been observed surfacing with the shells of large dead gastropods on their beaks, at least some of which contain fish prey (E.M.P. 2011 & J.M. 1997–2012, personal observations; [77]). This behaviour was previously referred to as conching with *Turbinella* sp. [77], but the shells used are actually those of the Australian trumpet snail (*Syrinx aruanus*) and the northern bailer (*Melo amphora*; E.M.P. 2011 & J.M. 1997–2012, personal observations; E. Krzyszczyk 2011–2012, personal communication). Considerable ambiguity remains regarding this behaviour and whether it qualifies as tool use.

(d) Other

Several instances of tool-use behaviour by aquatic animals do not clearly fall into any broad functional category. For instance, octopodes use water jets to deter scavenging fish, move unwanted debris and even to shoot human experimenters [14,42,43], whereas gray hermit crabs (*Pagurus pollicaris*) use sea anemones to aid in balance [16]. Two snail species move bits of sand along their propodium (foot) when inverted, which eventually helps to right the animal, but such behaviour could just be the result of their normal locomotory movement and might not qualify as tool use [66]. Some marine mammals use objects in other contexts. Sea otters sometimes wrap themselves in kelp, which aids in buoyancy and helps maintain their location during rest [44]. Amazon river dolphins (*Inia geoffrensis*) occasionally carry sticks, rocks, lumps of clay and/or shells, which is hypothesized to be a socio-sexual display [60], and humpback dolphins (*S. chinensis*) throw shells during social play [64], but for both behaviours, the function of the object use is not currently well understood.

3. Physiological and ecological factors specific to the aquatic environment

Similar to some land-based animals [78–81], several aquatic taxa have specific physiological adaptations or tendencies that predispose them to tool use. For example, archerfish have a modified mouth morphology that aids in water shooting [82], many crabs have specialized hair-like structures (setae) that securely hold objects [48], and sea otters have retractile claws on their forelimbs and object-carrying pouches between their forelimbs and chest [83]. However, most adaptations for life in the water do not promote the use of tools and instead result in an efficient streamlined body plan that generally lacks appendages capable of manipulation. In fact, many characteristics of aquatic environments help explain why tool use is comparatively rare in water, observational biases notwithstanding. For example, buoyancy counteracts gravity, meaning that not only are animals lighter, but so are potential tools, making them less useful. Furthermore, given the movement and viscosity of water, striking or even controlling objects underwater is more difficult than in air (especially elongated objects, see Gowlett [84]). Finally, aquatic and especially marine habitats are much more three-dimensional and have fewer objects than land-based habitats, where substrates and objects are plentiful. Thus, merely by living in water, aquatic animals have few opportunities and less physical ability to use tools.

Nonetheless, among aquatic organisms benthic animals tend to have the ecological conditions most likely to favour tool use: a hard substrate, available objects, small home ranges, less streamlined morphology and greater manipulative ability. Many non-benthic animals will, in fact, never see the substrate or come into contact with any objects besides floating debris or other pelagic organisms. It is not surprising then that most tools used in water originate from the benthos, even kelp, which sea otters use at the water's surface (table 1). This is very similar to how non-aquatic animals (including birds) tend to use tools on terra firma (St Clair & Rutz [8] and Teschke *et al.* [85]). In fact, terrestrial living has been proposed as a major factor driving tool use among primates [86]. Unlike arboreal habitats, terrestrial environments offer a larger number of substrates and objects, and terrestrial living allows for tool re-use, opportunities for combining tools and cumulative technology (reviewed in [86]). Thus, both on land and in water, the adaptive value of tool use and its presence depend greatly on the specific ecological conditions animals face [87].

4. Cognition, learning and culture

Like on land, the presence of tool use among some aquatic animals appears to require learning and higher cognition, whereas in others, learning may not be required but may improve tool-use efficacy. The majority of decorating behaviours by crabs and urchins are likely innate and require little learning [57]. In fact, many decorating behaviours are obligate [48], and crabs that have been blindfolded and whose brains have been functionally disconnected from their appendages, still perform the behaviour [53,88]. Among archerfish, learning is probably not required for the tool use, but does allow fish to account for changes in temperature, salinity and the location and size of their prey. Interestingly, fish learn much faster in the presence of trained conspecifics, which suggests social learning [37,89]. Captive largespot river stingrays (*Potamotrygon castexi*) learn to extract food from plastic tubes using water jets [32], which may illustrate problem-solving abilities that are common among fish, but for most cases of fish tool use, additional studies are required to determine the role of learning.

The bigger-brained tool users, cephalopods, sea otters and cetaceans, show substantial flexibility in whether or not they use tools and in the types of tools they use, evidence that the occurrence of tool use depends on learning. Cuttlefish learn to adjust their behaviour according to prey and use water jets only when necessary [14]. Octopodes demonstrate variable and impressive home construction [90], which, although not classified as tool use, is evident of their great flexibility in object manipulation. Many sea otters have never been observed using tools and instead target soft-bodied prey [69]. Among tool-using otters, variation in tool type and use exists with otters spending 0.3–21% of their time using tools [69], depending on their prey type (snails may require tools) and sex (females without pups use tools more than females with pups and males [69]). Like archerfish, sea otters also improve their tool use performance with experience [91]. In fact, sea otters appear to learn to use tools primarily through vertical social transmission, with pups adopting the same techniques, tools and diet as their mothers [91–93].

Among cetaceans, there is considerable variation in the occurrence of tool use within and between populations. Humpback whales engage in bubblenet feeding at several sites but not all, and it is currently unclear how widespread the behaviour is in each population [27]. In Florida Bay, only bottlenose dolphins that use shallow sand banks engage in mud-ring feeding [40], and in Shark Bay, many dolphins that inhabit the same channels as spongers do not sponge forage [4]. Those dolphins that do adopt sponging learn the behaviour from their mothers and then almost exclusively forage using sponge tools throughout their lives, showing extensive lifetime learning with a peak in efficiency at mid-adulthood [74,93,94]. However, not all dolphins born to spongers adopt the behaviour even though both sexes are philopatric [95]. Presently, over 90% of daughters born to spongers use sponge tools, compared with only 50% of sons (higher than reported in [4]), which results in a female sex bias [4]. Furthermore, female spongers engage in the behaviour more than males (mean proportion of activity budget ± s.e.: $n = 12$, adult females $= 0.44 \pm 0.05$, $n = 4$, adult males $= 0.22 \pm 0.02$, $z = 2.15$, $p = 0.02$, permutation test, 10 000 permutations, 372 h of focal observation) and even use tools more than any other animal, save humans [4]. Sponging also appears to have either been innovated multiple times, or horizontally socially transmitted. Subpopulations of spongers exist in the western [96] and eastern gulfs [4] of Shark Bay, and come from multiple matrilines [96]. In addition, we recently discovered a new group of spongers at a site (30–50 km) between the two gulfs (Point Peron), which may indicate an additional innovation event or provide a missing link between the two gulfs. Yet simulations show that if horizontal transmission and/or multiple innovation events did occur, then they did so at very low frequencies [97], which is not surprising given that female spongers have not been sighted further than approximately 6 km from their channels, except when being consorted by males.

On land, when tool use requires learning, it is often associated with social tolerance, prolonged development and relatively larger brain size or elaborated cognition within taxa ([85,93,98,99] although see Haslam [100]), but because of the scarcity of data in aquatic habitats, systematic phylogenetic comparisons are not yet possible (but see [70]). However, generally more cognitively complex tool use is characterized by tool manufacture [101], tool composites [102], tool re-use [102], cultural transmission [103] and cumulative technologies [86]. Several of these features are present in the aquatic tool users, particularly those with large brains. Humpback whales expel bubbles in a carefully constructed net [45], and bottlenose dolphins stir up mud in a consistent ring shape [40], both of which may be examples of aquatic tool manufacture. Sea otters use tool composites (one rock as an anvil, and another as a hammer) [2], and octopodes sometimes use two halves of a coconut shell to construct their protective shelter [15]. Sea otters, octopodes, crabs, fishes and dolphins all show tool re-use. Sea otters use the same tools to extract multiple prey items [2], and octopodes carry their coconut shells for later deployment [15]. Some crabs re-use the same anemones or objects for protection from multiple threats [12], and whitetail majors probably re-use some of the same sand when cleaning nest sites [24]. Dolphins that sponge often retrieve their tools after each prey capture and use the same sponge for up to several hours (average 59 ± 43 (s.d.) min, min. $= 1$ min, max. $= 3.5$ h, $n = 266$ sponging bouts, updated from that reported in [72]). Only one case of tool use by aquatic animals has thus far been considered ‘cultural’—sponging by dolphins. In addition to being socially learned, sponging serves an affiliative function that distinguishes subgroups, or subcultures of spongers and thus meets both requirements for culture [104]. We have recently shown that spongers preferentially associate with other spongers and form strong cliques [104], and thus may horizontally learn about sponging from each other. Thus, while more data are required, some aquatic tool use is indicative of cognitive complexity as it often is for primates and birds [7,93,98].

5. Is aquatic tool use distinct?

Even though tool use is rare in aquatic systems, the types of tools that are used distinguish it from land-based tool use. Aquatic tool users use living animals or their products as tools more than land animals. Many filter-feeding marine animals are sessile and thus ‘available’ as tools, and aquatic animal products such as shells do not deteriorate quickly. By contrast, land-based animals rarely use other animals or their products as tools, in part, because such objects likely deteriorate quickly, but also because of the ample availability of objects derived from plants [5,8,84,85]. Aquatic animals can also manipulate their surrounding environmental medium (water) more easily than land-based animals. In fact, over half of the cases of tool use by aquatic animals involve the use of water as a tool (table 1). This is not to say that land-based animals cannot manipulate their environmental medium (air) to some degree. For example, honeybees (*Apis mellifera*) fan air to cool their hives [105] and deter predators [106], and many other animals likely blow or fan air for a variety of functions, but as with fish egg-fanning, the object is unclear and such behaviours are not usually considered tool use.

Among dolphins and sea otters, the aquatic animals whose tool use we know the most about, two additional features stand out. First, although individual-level foraging/resource specialization, defined as the use of a narrower niche than the population niche [107,108], occurs among many invertebrate and vertebrate taxa both on land and in the water [107,109], individual-level specialization in tool use is rare. To the best of our knowledge, the only documented cases outside of humans occur among sea otters [69] and bottlenose dolphins [4]. Most bottlenose dolphins never use sponge tools, but nearly all that do specialize in the behaviour and spend approximately 96% of their foraging budget using sponge tools [4]. Similarly, many sea otters do not use tools, but those that do, use tools so often that they generalize the behaviour to the occasional prey item that does not require tools [69]. There is even evidence of further specialization within tool-using sea otters as some otters consistently use particular tool sets, tool types or techniques [2,92]. While land-based animals certainly vary in tool-use behaviour seasonally and between individuals [87,110–114] to the best of our knowledge, no individual-level tool-use specialization exists.

Numerous factors can drive interindividual variation in foraging behaviour [107,109], but in both sea otters and dolphins tool-use specialization by some individuals is likely driven by intraspecific competition and ecological opportunity [72,115,116]. In Shark Bay, the population density of adult females (approx. two dolphins per km^2) is at least twice that of the next densest site, Sarasota Bay, Florida [117], whereas sea otters in resource-limited sites show greater dietary specialization than those at sites where resources are abundant [115]. Thus, in both species, the need to reduce competition and exploit a unique niche may have led some individuals to use tools to forage. In similar scenarios on land, tool-use behaviour often spreads horizontally throughout the population, and little individual-level specialization evolves (e.g. primates [118] and Chappell *et al*. [119]). In fact, among Bossou chimpanzees, some offspring of non-tool-users do use tools, suggesting that non-vertical social transmission occurs even though the sensitive learning period of 3–5 years (similar to that for dolphin tool use) occurs when they are primarily with their mothers [114,120]. However, in aquatic systems horizontal social transmission is unlikely for several reasons. First, water currents likely wash away tool artefacts and even those heavy enough to remain stationary are eventually buried by sediment. Second, the low cost of travel in water (e.g. [121]), and the vast openness of most aquatic habitats allows for greater dispersion during foraging, making tool use a solitary activity [4,104]. Thus, in aquatic habitats, naive individuals rarely observe others using tools and/or encounter tool products, which is in contrast to some cases of land tool use where individuals regularly visit tool-using sites and forage with tools in groups [87,118,122]. In fact, Fragaszy *et al*. [114] propose that artefacts and tool-use sites may act as a spatio-temporal extension of social support for promoting tool-use learning in young individuals. It is not surprising then that for at least dolphins and sea otters vertical social transmission seems to be so important (also see discussion of importance of vertical transmission in Meulman *et al*. [93]). Only offspring of tool-using dolphins and otters are exposed to tool artefacts and have opportunities to repeatedly observe tool-use behaviour during their formative years. It seems then that the dynamic and expansive nature of aquatic habitats hinders the horizontal transmission of tool use, leaving vertical transmission as the primary mode of social learning, which ultimately promotes individual specialization.

Matrilineal transmission of tool-use specialization in both dolphins and sea otters may also explain the observed female sex bias, which is observed in some cases of land-based tool use (e.g. female bias in genus *Pan* [110,123,124]), but not others (male bias for genus *Cebus* [125,126]). In Shark Bay, females tend to use and specialize in rare hunting tactics more than males, such as beaching [127] and sponging [4], many of which are maternally socially transmitted to primarily female offspring [94], presumably because foraging specialization is too costly for males [4]. Sponging in the eastern gulf is restricted to an approximately 28 km^2 area, which is less than half the size of a typical male home range (approx. 76 km^2), and a little over one-fourth the size of a combined male alliance range (approx. 96 km^2) [128]. Thus, if males were to adopt sponging, then it would severely restrict their ranging and ability to form and maintain their alliances, which are necessary for successful reproduction [129]. In sea otters, a similar situation may exist due to sex segregation [130], but the sex differences in otter tool use have only recently been uncovered [69] and deserve further investigation.

6. Conclusion

While tool use among land-based animals has long been of interest to biologists, anthropologists and psychologists alike, such behaviour in aquatic systems has received little attention. In our review, we found tool use by aquatic animals to be rare, partly due to observational biases, but also because their physiology and ecology are not amenable to tool use. That being said, echinoids, crustaceans, cephalopods, marine mammals, fishes and possibly gastropods demonstrate tool use, primarily in foraging contexts, similar to land-based tool users. We expect tool use to be rare given the different challenges aquatic animals must overcome compared to land-based animals, so the absences of tool use among many aquatic organisms should not be viewed as a lack of ability, but rather a lack of need. For example, although delphinids are larger-brained than primates (save humans [131]) and thus might be expected to engage in substantial tool-use behaviour, they have a highly sophisticated echolocation system and probably have very little need for tools (also see discussion in Meulman *et al*. [93]). Nonetheless, the tool-use behaviours that do exist among aquatic animals provide insight into the specific conditions that favour tool use and help us understand its adaptive value and evolution across all environments.

Acknowledgements. We are grateful to Dora Biro and all of the participants in the Royal Society meeting on ‘Tool-use as adaption’ for stimulating discussions on tool use across different species. Our colleagues on the Dolphins of Shark Bay Research Project, particularly Ewa Krzyszczyk, Quincy Gibson and Brooke Sargeant, contributed data that we have summarized here. We are grateful to Jane Fromont for identifying sponge species.

Funding statement. We also thank the following funding sources for our research: Georgetown University, NSF 0941487, 0918308, and ONR 10230702.

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