# Can fishes build things?

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When biologists want to give examples of animals being able to build things, fishes don't readily come to mind. It's understandable. Fishes have a hard time building things because they are ill-equipped for the job. Unlike land vertebrates, they don't have digits with which to hold things. They can only shovel earth with their fins, or carry earth and small objects in their mouths.

Yet, some fishes do build things. Their methods can be classified into three categories:

- 1) Excavations: digging up depressions or burrows in gravel, sand or mud;
- 2) Pile-ups: piling up sand, pebbles, mud, shells or twigs to build mounds or simple walls;
- 3) Gluing: sticklebacks use kidney secretions to glue plant bits together and form nests for their eggs, while gouramis and some armoured catfishes use mucus to create bubble nests.

Following are some specific examples of building in the fish world.

## The burrows, turrets and walls of mudskippers

Let's start with mudskippers – a group of 25 species from the goby family. Found on the coastal mudflats of Africa, Southeast Asia and Australasia, they are well adapted to an amphibious lifestyle. They are also good excavators. Using their mouths to carry mud, they dig up burrows that can be as much as 2 m deep (about 6 feet), though most reach only half that depth. The burrows are shaped like a J, or, when they have two entrances, like a Y. (Burrow shape can be determined by pouring resin into the burrow and making a cast of it, after having flushed out the resident of course.) Mudskippers stay in their burrow at high tide, when the mudflats are under water, so as to avoid the predatory species that cruise the shallows. At low tide, they emerge and go about their business on the exposed mud, but they are wary and retreat to their burrows at the least sign of danger.<sup>1</sup>

At least two species, the giant mudskipper *Periophthalmodon schlosseri* and the walking goby *Scartelaos histophorus*, build a special chamber at the bottom of their burrows into which they carry mouthfuls of air. Once released the air accumulates at the top of the chamber and forms a reserve from which the fish can breathe – like all amphibious fishes, mudskippers are good air breathers. The usefulness of this air

reserve must be related to the fact that water in the burrow typically contains little oxygen.<sup>2</sup>

Two other species, *Periophthalmus argentilineatus* and *Periophthalmus minutus*, build mud turrets several inches high around the entrance of their burrow. They do this by depositing mouthfuls of mud. The role of these turrets is unclear. They may constitute observation posts from which the fish may check for the presence of predators before "stepping" onto the mudflats, or, given that the water in the turrets is warmer than in the burrow, they may act as little saunas where the fish can warm themselves up and activate their metabolism before the day's activities.<sup>3</sup>

Mudskippers maintain territories around their burrows. When the population gets crowded, little mud walls a few inches high start to appear at the territorial boundaries. At the highest densities, continuous walls delimit polygon-shaped territories. The whole mudflat looks like a mosaic of mostly pentagonal and hexagonal-shaped enclosures, each slightly less than 1 m (3 feet) wide. The walls are several inches high and made from piled-up mouthfuls of mud. They keep aggressive interactions between neighbours to a minimum ("out of sight, out of mind"). When mischievous researchers knock down walls, mudskippers assiduously start to rebuild them, but until the fortifications are completed there is a measurable increase in hostility between neighbours. Fortunately, in summer the mud walls harden under the hot baking sun and can last up to several months, even though they are regularly exposed to the tides.<sup>4</sup>

# The burrows of red band-fish, Cepola rubescens

The technique of pouring resin down a burrow to obtain a cast has also been applied to the red band-fish off the coast of Lundy, an island in the Bristol Channel, UK. The red band-fish has a long ribbon-like body, well suited to burrow living. The fish studied at Lundy were 12 to 74 cm long (about 5 to 29 in) and lived on the sea bottom at a depth of 10-20 m (about 33-66 ft). There they excavated burrows in mud. Researchers cast a total of 13 burrows (after chasing the occupant away with a narrow rod) and dipped a ruler into 117 more. <sup>5</sup>

The burrows turned out to be single shafts with a funnel-like entrance and an enlarged section at the bottom. Their mean depth within the sediments was 49 cm (19 in). The deepest burrows, which belonged to the largest males, were up to 1 m deep (3 ft). The shafts were mostly vertical but lateral deflections were sometimes forced by the presence of buried stones or shells. Many of the burrows featured a side branch at mid-depth, pointing slightly upward. In cross section the burrows were elliptical, with enough room to allow pectoral fin movements and body undulations.

Some fish were captured and taken into captivity where their burrowing behaviour could be observed. The fish excavated using their mouth, though they also sometimes pushed the mud aside with their body. Mouthfuls of mud were dumped no more than a body length away from the entrance. Between bouts of mud transport the fish

regularly "coughed": they opened their gill covers and forcefully passed water through the gills to dislodge any mud particles trapped in them.<sup>6</sup> After 6 h of hard work the burrow was deep enough for the fish to hide completely inside. Further field and laboratory work showed that even when a burrow is finished, maintenance work is still necessary to prevent siltation and to repair collapsed areas. The fish do this work mostly at dawn and dusk.

It has been calculated that up to 6 liters (about 1.5 gallon US) of sediments can be displaced by the construction of one large band-fish burrow. For an average-size burrow, the volume is 3 liters.

## The roofed burrows of yellowhead jawfish, Opistognathus aurifrons

This small fish (maximum length 10 cm, or 4 in) builds burrows 11-22 cm deep (about 4.5-9 in) in rubbly sand. The burrow usually takes the shape of a chamber excavated underneath a rock, or a chamber lined with coral fragments to solidify it in the absence of a rocky roof. One individual was filmed in the wild building a new burrow after a large pebble fell into the entrance of its former home (the fish had tried to dislodge the obstacle, but without success).

Using its mouth the jawfish first excavated a funnel-shaped crater, 10 cm deep (this measure included the height of the rim formed by the displaced sand). Then, again using its mouth, it carried and dropped pebbles into the crater, slowly filling it, all the while maintaining a central vertical tunnel that gave access to the bottom of the hole. It then alternated bouts of pebble carrying with the excavation of a chamber at the bottom end of the tunnel. Eventually the chamber was complete and the crater above was full of pebbles except for the masonry-lined central tunnel. Together with small buried rocks, the pebbles formed a solid roof for the chamber. Finally, the fish covered the pebbles at the surface with sand. The whole operation took 8 h to complete.<sup>7</sup>

# The burrow of the convict blenny ( = engineer goby, = convict fish), *Pholidichthys leucotaenia*

This fish from the southwest Pacific can be up to 50 cm (20 inches) long. It is shaped like an eel and adults live in male-female pairs in single burrows dug in coral reefs. The burrow is in fact a labyrinth of tunnels, estimated to be as much as 6 m long (20 feet). And it needs to be that big because it also shelters all the young the pair produces. At dawn, hundreds of young, each 1-10 cm long (0.4 to 4 inches), leave the burrow to feed on plankton in the water column. During that time, the parents clear the burrow of sand and debris, spitting out as much as 3 kilos (6.6 pounds) of sand in a single day. At dusk, the young stream back inside the burrow through its single entrance. At night, the young hang from the ceiling of the tunnels, suspended by a thread of mucus stuck to their head (this was observed by inserting an endoscope – a

flexible tube of fiber optics equipped with a lens at one end and a camera at the other - inside some of the burrows).

It seems the parents never leave their burrows; so how do they feed? Nobody knows for sure, but hypotheses include micro-organisms living inside the sand the fish dig out, old mucus threads and faeces produced by the young, or even food regurgitated by the young to their parents. For more information, see the following web sites:

http://ngm.nationalgeographic.com/ngm/0506/resources\_cre.html

http://www.mote.org/index.php?src=directory&view=magazine&refno=56&srctype= magazine\_detail

<u>http://www.youtube.com/watch?v=gTlPFG6\_Ly8</u> From episode 4 of the Life series produced by the BBC.

# The spawning chamber of the moga ( = Nicaragua cichlid), *Hypsophrys* nicaraguensis ( = Cichlasoma nicaraguense)

At the 2007 Cichlid Classic meeting in Chicago, researcher Ron Coleman reported the following observation he made in the field. He found moga eggs lying at the end of a foot-long (30 cm) tunnel – such a deep nest may explain why the eggs are non-adhesive, an oddity among New World cichlids. He also observed some of these fish in the act of digging the tunnel: they were spinning inside, like a living drill. The dorsal fin of the spinning fish raked the side of the tunnel, enlarging it.

# Various examples of mounds

Six families of fishes – cyprinids, gobiids, malacanthids, cichlids, tetraodontids, and labrids – include species that build mounds.

<u>Cyprinids</u>: In North American streams, the male cutlip minnow *Exoglossum maxillingua*, 90-115 mm long (3.5-4.5 in), assembles mounds that are 75-150 mm high (3-6 in), 30-45 cm in diameter (12-18 in), made up of more than 300 pebbles 13-19 mm in diameter (a quarter to half an inch). The fish carry these pebbles one by one in their mouths, sometimes stealing some from the mounds of other males. The females deposit their eggs on the upstream slope of the mounds, and the males cover these eggs with more pebbles. Males of the hornyhead chub *Nocomis biguttatus*, 90 mm long (3.5 in), and of the river chub *Nocomis micropogon*, 100 mm long (4 in), also build mounds during the reproductive season. They start by clearing a slight depression in the substrate, which they overfill with up to 10,000 pebbles until the mounds are 60-90 cm (2-3 ft) long (in the direction of the water current), 30-90 cm wide (1-3 ft), and 5-15 cm high (2-6 in).<sup>8</sup> Females lay their eggs among those pebbles. They are presumably impressed by the biggest mounds, as these are built by the biggest and strongest males. The stone accumulation is free of sand and it exposes the eggs to a good water current that supplies oxygen.

<u>Gobiids</u>: Gobies of the genus Valenciennea live in male-female pairs that excavate and share burrows. Several burrows can be present within the same territory. They are used as refuge, as a sleeping place, and also as a place to tend eggs during the reproductive season. Coral rubble is often heaped by the fish over the burrow entrances. In a Red Sea population of twostripe gobies *Valenciennea helsdingenii*, such mounds were found to be as high as 30 cm (about 1 ft), with base diameters of 25-60 cm (about 2-3 ft). Not bad for a pair of fish that was only about 15 cm (6 in) in length! A team of divers led by ichthyologist Eugenie Clark, of the University of Maryland, removed approximately half of a medium-size mound and counted no less than 4062 individual pieces of coral rubble, shells, and shell fragments (so double that number for the whole mound). There were also a few odd pieces such as worm tubes, egg cases, and even one watermelon seed! While building their mounds, goby pairs could collect and carry as many as 9 pieces of coral rubble per minute.<sup>9</sup>

In the long-finned goby Valenciennea longipinnis, pairs build a mound over one of the two entrances of their spawning burrow. This mound, 6-13 cm high (about 2.5-5 in), helps ventilate the burrow. The mound deflects water currents, which increases water speed in that spot, which in turns lowers pressure. Pressure is therefore lower at the entrance surrounded by a mound than at the other entrance. This pressure differential generates a water flow within the burrow. This is particularly useful during the parental phase, as the water flow can supplement the fanning done to the eggs by the caring male. This functional role of mounds was demonstrated by Takeshi Takegaki and Akinobu Nakazono of Kyushu University. The two scientists injected ink at the mound-less entrance of burrows and observed that the ink was quickly sucked into the burrow and soon percolated through the mound at the other end. When the mound was removed, the ink took longer to come out. Also, the concentration of oxygen was found to be higher in burrows with mounds than in burrows whose mounds had been removed. Takegaki and Nakazono reported that over the four days of the parental phase, males stayed inside their burrows to fan the eggs while females stayed outside to maintain the mounds. When females were experimentally removed, the mounds soon lost their height, and many males perhaps discouraged by the impoverished ventilation of their burrow - abandoned their breeding attempt and ate the eggs they were caring for.<sup>10</sup>

<u>Malacanthids</u>: At least five species of tilefishes build mounds of coral rubble over the entrance of their burrows: *Hoplolatilus fronticinctus*, *H. geo*, *H. pohle*, *Malacanthus brevirostris*, and *M. plumieri*. The mounds can be as high as 80 cm (31 in) and their oval-shaped base can cover as much as 2 x 3 m (about 6 x 9 ft). From partial sampling it has been estimated that the largest mounds contain as many as 200,000 individual pieces of coral rubble. Such mounds are probably the largest built structures in the fish world, but even for tilefish they represent an extreme. In one study of 33 mounds built by *M. plumieri* (the sand tilefish) off the coast of Colombia,

the minimum size was 85 x 67 x 15 cm, the maximum was 208 x 198 x 17 cm, and the average was 133 x 102 x 22 cm (52 x 40 x 9 in). The fish themselves were about 20-50 cm long (8-20 in). The mounds, and of course the burrows associated with them, may offer protection against predators such as sharks. <sup>11</sup>

<u>Cichlids</u>: Males of many mouthbrooding cichlid species in Lake Malawi and Lake Tanganyika, Africa, build sand cones that are flattened or crater-shaped on top. These mounds are sometimes called bowers, because like the elaborate constructions of bowerbirds they are solely meant to attract and impress females.<sup>12</sup> They do not provide shelter for the fish nor for their eggs. Some of these sand mounds are huge: they can reach 3 m in diameter (10 ft) and 40 cm in height (16 in). The males themselves are all under 25 cm in length (10 in).<sup>13</sup> Some females seem to prefer to mate with males whose sand mounds are bigger and/or with a rim of even height, suggesting that good building is taken as a sign a good genetic quality or good health.<sup>14</sup> However, in some species there is no preference for bigger sand castles, and for them it has been argued that the structure allows species recognition (Lake Malawi and Lake Tanganyika contain complexes of numerous and very similar-looking cichlid species).<sup>15</sup>

<u>Tetraodontids</u>: Male pufferfishes *Torquigener* sp. also build sand mounds to attract females. The mounds are circular, up to 2 m in diameter, and quite beautiful, showing a radiating pattern of ridges and valleys. You can view the fish building their mounds at <u>http://www.youtube.com/watch?v=MciAVgTuIGM</u> and read the scientific report at <u>http://www.nature.com/srep/2013/130701/srep02106/full/srep02106.html</u>. <sup>16</sup>

Labrids: Many wrasses sleep buried in sand at night. Around the time of sunset they dive into loose sand and spend the night there. Two species go the extra mile and make sleeping mounds (or sleeping nests). The Jordan's tuskfish *Choerodon jordani* uses its head to scrape out sand from under coral rubble, and then it adds coral fragments over the site. It slips into this nest just after sunset. For its part the rockmover wrasse *Novaculichthys taeniourus*, 14-26 cm long (5.5-10 in), carries sand in its mouth to make a small mound which it covers with pieces of dead coral. Then it moves a few pieces of coral aside and dives into the sandy mound, where it spends the whole night. The coral bits presumably hinder or deter nocturnal predators. A single fish can make more than one such mound every evening, spending an average of 34 minutes on the task. Larger individuals have the gall to steal the sleeping mounds of smaller fish at sunset, and that's probably why some fish make more than one nest. <sup>17</sup>

## **Depression nests**

Many fish species dig up and clear a depression in the substrate where the female will lay her eggs and where the young will be defended. Examples include the male bowfin, *Amia calva*, which cuts or pulls out all reeds in a circular area 38-60 cm (about 15-24 inches) in diameter; and the male smallmouth bass, *Micropterus dolomieui*, whose nest can reach 185 cm (6 feet) in diameter.<sup>18</sup>

In preparation for laying their eggs (which will not be defended later on), female Pacific salmon use their fin to dig large bowl-shaped pits in gravel. In the case of a very big Chinook salmon, these depressions can be 0.4 m deep (a foot and a half) and cover an area the size of two parking lot stalls. It has been estimated that salmon spawning in southwestern Alaska disturb 30 % of the available streambed in this manner –and this is in populations that are not at their peak numbers, since they are fished commercially.<sup>19</sup>

#### **Vegetation nests**

Male threespine sticklebacks, *Gasterosteus aculeatus*, build vegetation nests at the beginning of the reproductive season. A male will start by digging a shallow pit in sand or mud with his mouth. Then he places slender pieces of vegetation in the pit. This material is glued together with mucus secretion from the male's kidneys. The gluing behaviour is easy to recognize, as the male swims over the nest with peculiar movements of the pectoral and anal fins, bringing his cloacal region in contact with the vegetation. When enough material has accumulated, the male starts pushing his snout into the heap. Eventually the male creeps through the heap, forming a horizontal tunnel. It takes him about five hours to build such a nest. A study in the U.K. has found that nest characteristics (number of pieces used, area of the nest, total mass) differ between males but are consistent within males.<sup>20</sup>

During spawning the female swims through the tunnel and deposits her eggs there. The male follows to release his milt. The male then guards the nest and fans water into the entrance to bring oxygen to the eggs. Sometimes he pokes holes into the nest walls, presumably to allow better water circulation during fanning.

Other stickleback species build nests in a similar fashion. There is a twist in the case of the ninespine stickleback *Pungitius pungitius*. Here the male builds his nest off the ground, among the branches and leaves of aquatic vegetation. He also displays a particular gluing behavior in addition to the "standard" one. First he bends his head and tail towards each other. A drop of glue is extruded from the cloaca, forming a thread which the fish grabs in his mouth. He then bores into the mass of vegetation pieces he has accumulated and deposits the thread there. This probably helps to consolidate the inside of the nest.

The male sea stickleback, *Spinachia spinachia*, starts his nest by laying down a network of glue threads in a dense patch of seaweed. Then he adds pieces of vegetation to the matrix until a spherical mass of material is obtained. <sup>21</sup>

A few other fishes beside sticklebacks make vegetation nests, though glue does not seem to be involved in the building process. For example the aba, *Gymnarchus niloticus*, makes a floating nest from weeds that it uproots or nips free. The nest can be 0.5-1.0 m long (20-40 in). The female lays her eggs inside this mass of plants and the male subsequently guards it.

#### **Bubble nests**

Male gouramis (anabantoids) are well known for their capacity to produce floating bubble nests. Some armoured catfishes from the family Callichthyidae can also produce foam nests. In all cases the bubbles or foam are produced by mixing air with mucus in the fish's mouth. The mucus makes the bubbles stick together. Bits of plants are often incorporated into the bubble nest. The eggs released by the female in midwater are picked up by the male, who spits them into the mass of bubbles. The male then guards the nest. If any egg falls down from the nest, the male picks it up in his mouth and spits it back into the nest.

<sup>3</sup> Lee, H.J., and Graham, J.B., September 2002, Their game is mud, Natural History 111: 42-47.

<sup>4</sup> Clayton, D.A., 1987, Why mudskippers build walls, Behaviour 102: 185-195; Clayton, D.A., and Vaughan, T.C., 1986, Territorial acquisition in the mudskipper *Boleophthalmus boddarti* (Teleostei, Gobiidae) on the mudflats of Kuwait, Journal of Zoology (London) 209: 501-519.

<sup>5</sup> Atkinson, R.J.A., and Pullin, R.S., 1996, Observations on the burrows and burrowing behaviour of the red band-fish, *Cepola rubescens* L., Marine Ecology 17: 23-40.

<sup>6</sup> Apparently the swordtail jawfish, *Lonchopisthus micrognathus*, has another means of cleaning its gills after a bout of digging : it can insert its tail into the gill chamber through the opercula! And speaking of special adaptations: some digging gobies are capable of ejecting their mouthful of sediments directly through the opercula; so, while digging headfirst inside a shallow burrow, they can discharge the sediments without having to back out. See: Hansell, M., 2005, Animal architecture, Oxford University Press, Oxford.

<sup>7</sup> Colin, P.L., 1973, Burrowing behavior of the yellowhead jawfish, *Opistognathus aurifrons*, Copeia 1973: 84-90.

<sup>8</sup> Scott, W.B., and Crossman, E.J. 1998. Freshwater fishes of Canada. Galt House Publications Ltd., Oakville, ON; Wisenden, B.D., Unruh, A., Morantes, A., Bury, S., Curry, B., Driscoll, R., Hussein, M., and Markegard, S., 2009, Functional constraints on nest characteristics of pebble mounds of breeding male hornyhead chub *Nocomis biguttatus*, Journal of Fish Biology 75, 1577-1585; Bshary, R., Wickler, W., and Fricke, H., 2001, Fish cognition: a primate's eye view, Animal Cognition 5: 1-13, and references therein.

<sup>9</sup> Clark, E., Stoll, M.J., Alburn, T.K., and Petzold, R., 2000, Mound-building and feeding behavior of the twostripe goby, *Valenciennea helsdingenii*, in the south Red Sea, Environmental Biology of Fishes 57: 131-141.

<sup>&</sup>lt;sup>1</sup> Clayton, D.A., and Vaughan, T.C., 1986, Territorial acquisition in the mudskipper *Boleophthalmus boddarti* (Teleostei, Gobiidae) on the mudflats of Kuwait, Journal of Zoology (London) 209: 501-519.

<sup>&</sup>lt;sup>2</sup> Ishimatsu, A., Hishida, Y., Takita, T., Kanda, T., Oikawa, S., Takeda, T., and Khay Huat, K., 1998, Mudskippers store air in their burrows, Nature 391: 237-238; Lee, H.J., and Graham, J.B., September 2002, Their game is mud, Natural History 111: 42-47.

<sup>10</sup> Takegaki, T., and Nakazono, A., 2000, The role of mounds in promoting water-exchange in the eggtending burrows of monogamous goby, *Valenciennea longipinnis* (Lay et Bennet), Journal of Experimental Marine Biology and Ecology 253: 149-163.

<sup>11</sup> Büttner, H., 1996, Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia, Bulletin of Marine Science 58: 248-260; Clark, E., Pohle, J.F., and Halstead, B., 1998, Ecology and behavior of tilefishes, *Hololatilus starcki*, *H. fronticinctus* and related species (Malacanthidae): non-mound and mound builders, Environmental Biology of Fishes 52: 395-417.

<sup>12</sup> This use of the word "bower" for cichlids is contested: Tweddle, D., Eccles, D.H., Frith, C.B., Fryer, G., Jackson, P.B.N., Lewis, D.S.C., and Lowe-McConnell, R.H., 2004, Cichlid spawning structures: bowers or nests? Environmental Biology of Fishes 51: 107-109.

<sup>13</sup> The following article has a picture of a male *Cyrtocara eucinostomus* over its sand castle. The diameter of the mound is at least 7 times the length of the fish: McKaye, K.R., 1983, Ecology and breeding behavior of a cichlid fish, *Cyrtocara eucinostomus*, on a large lek in lake Malawi, Africa, Environmental Biology of Fishes 8: 81-96. The following book also has drawings of sand mounds: Keenleyside, M.H.A., 1979, Diversity and Adaptation in Fish Behaviour, Springer-Verlag, Berlin. See also: McKaye, K.R., Louda, S.M., and Stauffer, J.R. Jr, 1990, Bower size and male reproductive success in a cichlid fish lek, American Naturalist 135: 597-613, and references therein.

<sup>14</sup> McKaye, K.R., Louda, S.M., and Stauffer, J.R. Jr, 1990, Bower size and male reproductive success in a cichlid fish lek, American Naturalist 135: 597-613; Taylor, M.I., Turner, G.F., Robinson, R.L., and Stauffer, J.R. Jr, 1998, Sexual selection, parasites and bower height skew in a bower-building cichlid fish, Animal Behaviour 56: 379-384; Stauffer, J.R. Jr., Kellogg, K.A., and McKaye, K.R., 2005, Experimental evidence of female choice in Lake Malawi cichlids, Copeia 2005, 657-660.

<sup>15</sup> Barlow, G.W., 2000, The cichlid fishes: Nature's grand experiment in evolution, Perseus Publishing, Cambridge (Massachusetts).

<sup>16</sup> Kawase, H., Okata, Y., and Ito, K. 2013. Role of huge geometric circular structures in the reproduction of a marine pufferfish, Scientific Reports 3, article number 2106, doi: 10.1038/srep02106. See also: Bond, T., Muelle, R.J. and five others, 2020, Mystery pufferfish create elaborate circular nests at mesophotic depths in Australia, Journal of Fish Biology <a href="https://doi.org/10.1111/jfb.14506">https://doi.org/10.1111/jfb.14506</a>

<sup>17</sup> Takayanagi, S., Sakai, Y., Hashimoto, H., and Gushima, K., 2003, Sleeping mound construction using coral fragments by the rockmover wrasse, Journal of Fish Biology 63: 1352-1356; Nanami, A., and Nishihira, M., 1999, Nest construction by the labrid fish *Choerodon jordani* (Snyder 1908), Coral Reefs 18: 292.

<sup>18</sup> Scott, W.B., and Crossman, E.J., 1998, Freshwater fishes of Canada, Galt House Publ., Oakville.

<sup>19</sup> Moore, J.W., 2006, Animal ecosystem engineers in streams, Bioscience 56, 237-246. See also: Hassan, M. A., et al., 2008, Salmon-driven bed load transport and bed morphology in mountain streams, Geophysical Research Letters, 35, L04405.

<sup>20</sup> Rushbrook, B.J., Dingemanse, N.J., and Barber, I., 2008, Repeatability in nest construction by male three-spined sticklebacks, Animal Behaviour 75, 547-553.

<sup>21</sup> For more information on sticklebacks, see: Wootton, R.J., 1976, The biology of sticklebacks, Academic Press, London.