bouts irrespective of sex. This behavior seems to fit the play criteria and certainly warrants closer study. I have studied Vietnamese mossy frog tadpoles repeatedly 'riding' bubbles from an airstone at the bottom of a tall tank to the top. I have observed similar behavior in marine fish in a large very tall communal aquarium with such an air column. Here it is actually possible to be a bit anthropomorphic as the behavior does look as if it would be fun for us!

What about play in reptiles? Convincing examples of play have been found in lizards, turtles, and crocodilians. Komodo dragons, the world's largest lizards, engage in complex interactions with objects such as buckets, boxes, old shoes, and balls. In fact, sped up a little bit on video, their behavior is similar to that of dogs. They even play tug of war with their keepers over objects such as cans and handkerchiefs. Aquatic Nile soft-shelled turtles will bounce basketballs and floating bottles back and forth, manipulate hoops (Figure 1) and play tug of war with their keepers using hoses. North American Emydid pond turtles often engage in foreclaw titillation displays in social interactions with each other as hatchlings, behavior that otherwise is only found in sexual and sometimes agonistic encounters as adults. Crocodilians also engage in object play. A giant saltwater crocodile played with a basketball on a tether as part of enrichment. Although only a few papers have been published and cited in the references below, behavior patterns meeting the play criteria have been met.

If play is so widespread in the animal kingdom, how and why did this happen? Play is often found in the most intelligent and adaptable species, but we now know that it is not restricted to them. The presence of play facilitates novel and creative behavior, but this does not tell us about its origins. Indeed, play is so diverse and heterogeneous that no single factor can explain when and where it appears in the lives of animals. We also know little about the function of play in these animals, but as we are just beginning to get a handle on the function of play in mammals, our relative ignorance about fish, frogs, and reptiles is not surprising. But invertebrates play also — in fact, some of the best evidence for the function of play comes from work on spiders, where play was never observed until recently.

So, play, while very prominent in mammals and many birds, is relatively rare in other species. One proposal, termed Surplus Resource Theory, is that the origins of play are found in animals with sufficient metabolic resources for sustained activity and complex behavior that needs to be deployed in varying ways. They also need the time and safety to engage in behavior that may not be immediately advantageous, but through which animals learn or perfect behavioral skills, social acumen, physiological or perceptual abilities, and other means that enhance survival compared to non-playing conspecifics. On the other hand, in its ancient and more primitive incarnations, playing may not have had any specific advantage over non-playing, but eventually the benefits outweighed the often serious costs of play in energy and risks of injury and predation. A door has been opened, and exploring what lies beyond may be both fascinating and important.

Where can I find out more about play?

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Fun and play in invertebrates

Sarah Zylinski

Where should we look for playful invertebrates? The notion that invertebrates might indulge in play, and especially that they might have fun doing it, is generally met with scepticism. But given that the same was true of play in 'lower' vertebrates such as reptiles and fish until relatively recently, perhaps we shouldn't discount the possibility outright. So where should we look? Given that play is most frequently observed in large-brained vertebrate lineages, perhaps our first port of call should be the cephalopods. These large-brained molluscs are heralded as uniquely intelligent amongst the invertebrates, and their deep evolutionary split from the vertebrates provides us with a unique independent data point against which to investigate general trends in intelligence, cognition and, in this case, play. Shallow water coleoid cephalopods — octopuses, cuttlefish and squid — are well known for their capacity for complex learning and their flexible, complex behaviours. Their brains are comparable to vertebrates in relative size, with dedicated learning and memory centres analogous in many ways to the vertebrate cortex. On the flip side, cephalopods don't afford parental care to their offspring, are typically short lived (often one or two years), and are often semelparous (that is, they die after their first attempt at reproduction). Furthermore, the species considered to have the highest cognitive intelligence are solitary and show little or no social behaviour. What evidence is there then that cephalopods play, and more importantly, do they have fun doing it?

So do cephalopods play? When introducing my behavioural experiments with cephalopods in seminars, I often joke that there is nothing more demoralizing than being outsmarted by your experimental animal. Indeed, there are some individuals that seem to delight in being mischievous. For example, some cuttlefish use their siphons to squirt water at their keeper when impatient to be fed. However, there is currently

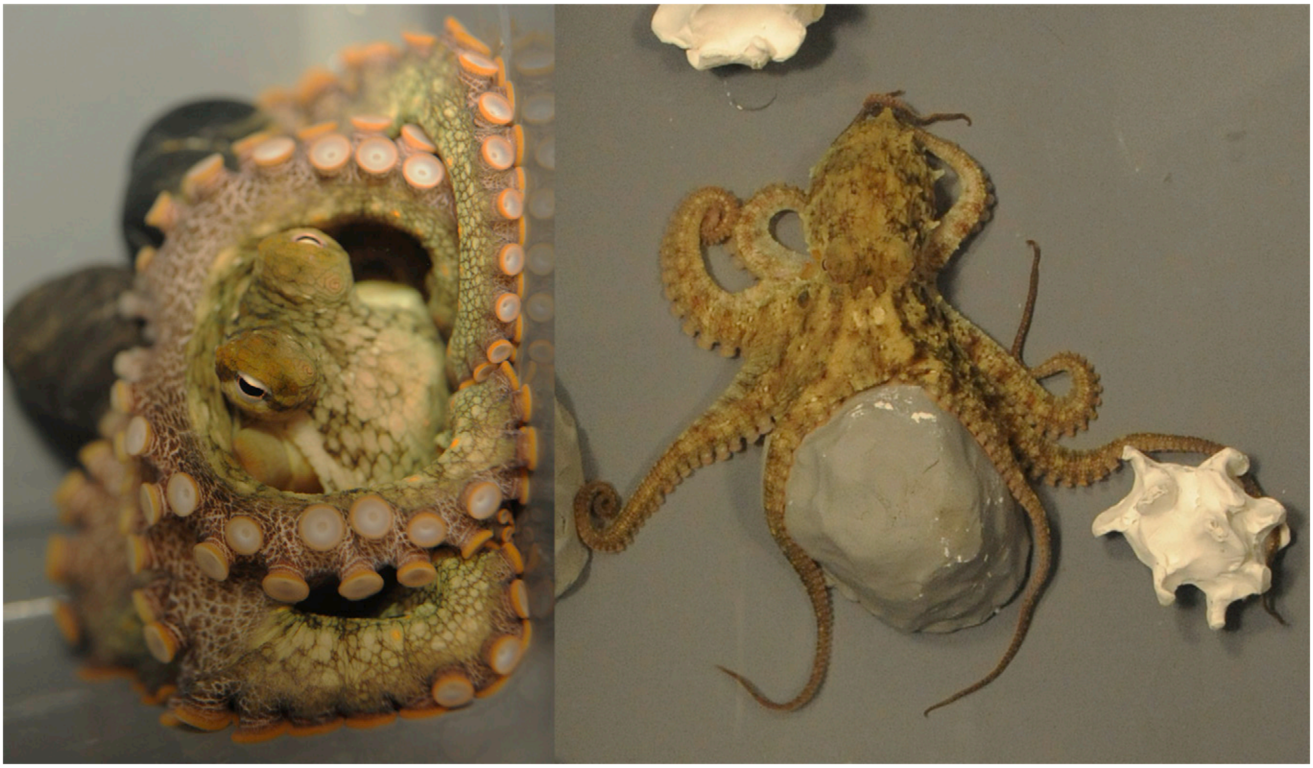

Figure 1. *Octopus bimaculoides* explores and interacts with novel objects in its environment. (Photo: S. Zylinski.)

no evidence for play in cuttlefish or squids as defined by Burghardt's (2005) five criteria: briefly, a behaviour that is incompletely functional, voluntary, modified from its regular form, repeated but not stereotypic, and initiated under stress-free conditions.

Among cephalopods, the strongest contenders for being animals that play are the octopuses, with their muscular arms which allow for more complex interactions with their surroundings (other SCUBA divers may have shared my unnerving experience of having a curious octopus attempt to wrestle the air-supplying regulator from their mouth!). Indeed, here we finally find published accounts of play in two species of *Octopus* from rather different habitats that do meet Burghardt's five criteria.

What are they playing at? To date, the only form of play demonstrated experimentally in octopuses is object play, which serves an obvious function in exercising muscle and nerve systems. For example, when encountering a novel non-food object, *Octopus vulgaris* shows a sequence of behaviours that moves from a "What is this object?" exploratory behaviour to playful "What can I do with this object?" interactions, involving manipulative behaviours such as pushing, pulling and towing. *Octopus dofleini* shows a similar sequence of behaviours, but uses its siphon, more typically used for jet-propulsion movement and removal of unwanted objects from its locale, to jet water at moving objects to engage in a playful activity not unlike repeatedly bouncing a ball.

I have watched a captive *Octopus bimaculoides* (Figure 1), once sated, pounce on a fiddler crab and then release it unharmed, repeating this release and recapture many times over, as a cat might with a mouse, and other people who have spent time observing octopuses have similar anecdotes of play-like behaviours. We might expect to see other forms of play in octopuses, but different types of play do not necessarily coevolve, so the presence of one type does not predict presence of another. Furthermore, octopuses are solitary so the absence of social play is unsurprising; perhaps future studies will uncover play-like behaviours in cephalopods such as *Loligo* or *Sepioteuthis* (squid and reef squid) that interact in loose shoals.

OK, but are they having fun? This is the million dollar question. We feel confident when we watch social play in mammals, such as dogs, that they are having fun, yet we also know fun is a very personal experience even within our own species. Personally, feeling any level of empathy for the emotional state of an octopus is far beyond my capabilities as a (reasonably) self-aware human.

What about fun and play in other invertebrates? There really aren't many examples beyond anecdotes. A strong case for sex play comes from the social spider *Anelosimus studisus*, where males and immature females engage in non-conceptive sexual behaviour, with both sexes gaining future performance-enhancing benefits from these mock copulations. Another example of arthropod play-like behaviour is found in the paper wasp *Polistes dominulus*. While in non-nesting aggregations young adult foundresses perform precocious dominance interactions that serve no immediate function, as they occur up to six months before colonies are founded and dominance hierarchies formed. This behaviour perhaps allows the wasps to assess their future dominance potential in a similar way to play fighting in young mammals. Anyone looking to find more examples of play-like behaviour in arthropods could probably do worse than to look for them in social insects.

Why don't we see more invertebrates playing? Play may have arisen in vertebrate lineages as a by-product of traits associated with the complex behaviours and cognitive abilities, in turn associated with increased brain size. Although we know that invertebrates are far from the mindless machines they were once considered to be, it might be that the neural architecture available to add new levels of control required for play is lacking, or the local solutions employed by invertebrates don't benefit from the adaptive advantages conveyed by play. Or perhaps it is simply that we are overlooking countless examples of play in invertebrates. For example, sex play may be more common in arthropods than we think: there are over 100 species of insect known to exhibit same sex courtship and/or copulation, often with no apparent immediate function. Moreover, a few years ago a study showing that sexually deprived male *Drosophila melanogaster* increased their ethanol intake led to headlines such as "Sexually deprived male fruit flies get drunk to ease the pain of rejection". This study highlighted that invertebrates can indulge in behaviours that are not useful in themselves, but which act on neural reward centres to attain something akin to pleasure, so perhaps the concept of invertebrate fun isn't so farfetched after all.

Where can I find out more?

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Primers

Playfulness and creativity

Patrick Bateson

Playful play is undoubtedly fun. Even so, many people think, incorrectly, that as they get older, they are no longer capable of such frivolous activity. They should heed George Bernard Shaw's advice: "We don't stop playing because we grow old, we grow old because we stop playing." The motivation to be playful comes from within. No external bribes are needed. In fact attempting to encourage such activity with food or money is likely to be counterproductive.

Having fun is a good reason to be playful. The pleasure it generates could be seen as its primary benefit. Even so, I want to explore what can be the longer-term benefits of playfulness. For the biologist, benefits are measured in terms of the particular ways in which an activity increases the chances of survival and enhances reproductive success. Most people would not worry too much if their playfulness affected their chances of survival and would probably not be at all concerned about its impact on their reproductive success. Many would, however, be interested in the particular long-term outcomes of their playfulness that eventually lead to those matters that concern biologists. I shall argue that one such outcome is their creativity.

Many composers, artists and scientists, famous for their creativity, were also remarkably playful. Wolfgang Amadeus Mozart was well known, notorious even, for his playfulness. The high-spirited pranks and jokes were also reflected in his music. For example his three-voice canon (KV559) consists of a nonsensical Latin text which when sung sounds like bawdy German. Pablo Picasso was once filmed painting onto glass. The onlooker saw the picture emerge, but viewed from the other side of the glass. Picasso started by quickly sketching a goat and then rapidly embellishing it. Other shapes appeared and disappeared; colours were mixed and transformed. By the end of the film the goat had long since gone and it would have been hard to say what the picture was all about. Picasso had been playing — probably showing off — but clearly enjoying himself hugely.

M.C. Escher wrote about his challenging designs in the following way: "I can't keep from fooling around with our irrefutable certainties. It is, for example, a pleasure knowingly to mix up two- and three-dimensionalities, flat and spatial, and to make fun of gravity." Famous products of this approach were his impossible staircases. The cartoonist Peter Brookes extended the fun when he represented Greek politicians endlessly seeking financial help from richer countries on a continuously ascending staircase.

The discoverer of the anti-bacterial properties of penicillin, Alexander Fleming, was famous for his playfulness. He was accused disapprovingly by his boss of treating research like a game, finding it all great fun. When asked what he did, he said that: "I play with microbes" and went on "… it is very pleasant to break the rules and to be able to find something that nobody had thought of." Another famously playful scientist and Nobel prize-winner was Richard Feynman. When he was getting bored with physics at an early stage in his career, he wrote: "Physics disgusts me a little bit now, but I used to enjoy doing physics. Why did I enjoy it? I used to play with it. I used to do whatever I felt like doing — it didn't have to do with whether it was important for the development of nuclear physics, but whether it was interesting and amusing for me to play with". He decided that he would play with physics again irrespective of how important it might be. Then while playing at work, every thing flowed effortlessly and he made fundamental contributions to nuclear physics.

Social play is marked by the cooperation between the partners. It is non-competitive and roles may be reversed. So individuals that are dominant in non-playful contexts may allow themselves to adopt a sub-ordinate role during play. Sometimes the playfulness is explicit. Jim Watson described the playful nature of scientific creativity when he and Francis Crick had set themselves the task of uncovering the structure of DNA. Their main working tool had been a set of coloured balls superficially resembling the toys of pre-school children. Watson wrote: "All we had to do was to construct a set of molecular models and begin to play — with luck, the structure