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Making an Ethogram for Octopuses: A Personal Story

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Making an ethogram, a repertoire of the behavior of a species or several related ones, is obviously an important foundation for any theoretical studies of their behavior. In addition, it is useful for conservation, and evolution, and as a basis for good care in captivity. But such a thorough description is neither easy nor quick. This account takes the reader on the author's journey through lab and field work on seven species and to the struggle to publish results that make up an ethogram of octopuses in the family Octopodidae.

Keywords: ethogram, octopuses

タコのエトグラムの作成：著者個人の体験談

ある種や近縁種の行動の目録であるエトグラムを作成することは、その種の行動を理論的に研究するうえで明らかに重要な基礎である。さらに、保全や進化の研究に役立ち、飼育下での適切な管理の基礎としても有用である。しかし、このような綿密な分析は容易ではなく、時間もかかるものである。この記録は、著者が 7 種類のマダコ科のタコについて、研究室とフィールドで研究を行い、エトグラムをまとめて結果を出版するまでの苦闘の道のりを、読者に伝えるものである。

キーワード：エトグラム、タコ

Elaboración de un Etograma para Pulpos: Una Historia Personal

La elaboración de un etograma, un repertorio del comportamiento de una especie o de varias especies afines, es obviamente una base importante para cualquier estudio teórico de su comportamiento. Además, es útil para la conservación y la evolución, y como base para un buen cuidado en cautiverio. Pero una descripción tan exhaustiva no es ni fácil ni rápida.Este relato lleva al lector al viaje del autor a través del trabajo de laboratorio y de campo con siete especies y a la lucha por publicar los resultados que conforman un etograma de pulpos de la familia Octopodidae.

Palabras clave: etograma, pulpos

The Story Behind Making an Ethogram

I made an ethogram for the near-shore octopuses (Mather & Alupay, 2016), and I was asked a few weeks ago where, why, how I did so, and did it take a lot of time and effort? This paper will answer these questions. The first concept to establish is what an ethogram is. The definition is "a catalogue or inventory of behaviors or actions exhibited by an animal," usually but not always a single species. Yes, it is a lot—everything an animal does. How could you describe 'everything?' Drummond (1981) suggested that one might look in five different domains, and the domain of actions with relationship to self seemed to me the most logical place to start. He felt that one would see regularities of topography of actions that would intuitively look like natural units.

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Where did the term and activity come from? It was begun by the ethologists in the 1930s, specifically by Lorenz and Tinbergen. At the time, behavior was studied by psychologists in the lab through experiments that mainly focused on rats and learning. This narrow view was famously challenged by Beach (1950), who pointed out that *Journal of Comparative Psychology* was actually *Journal of Rat Learning*. Ethologists were biologists who instead went to the field and looked at what animals were doing in their natural environment (Tinbergen, 1951). They expected to make an inventory of what they assumed were fixed and species-specific behaviors (Eibl-Eibesfeld, 1970). Schleidt (1974) carefully explained how the actions weren't very fixed, that a somewhat varying modal action pattern was a better descriptor, and that we tended to catalogue actions taking between one and ten seconds through a gestalt-like recognition process. Gosling (2001) emphasized that animals had personalities so not all individuals of one species behaved alike, and this clearly included octopuses (Mather & Anderson, 1993), so we needed to find average patterns with some variation in form.

Why do an ethogram? Well, how can you ask questions about behavior if you do not know what the animal does with its time? Basic research needs that backing—think of Tinbergen's four questions (evolution, function, development, structure), how can you investigate them if you don't know what the animal is doing in the first place? And when I started studying octopuses, we definitely did not know that, though we do not know a lot more now. Ethological assessment has recently become vital for many areas. It is important for conservation, for instance Gokula (2011) assayed the spot bellied pelican (*Pelecanus philippensis)* to help know how it was doing under protection (and see the elegant line drawings). An ethogram of different species can give you clues to evolution of the group, as Ruby & Niblick (1994) did for tortoises. But ethograms are vital for proper care of captive animals, such as in zoos and agriculture. How can you care for an animal if you do not know when its behavior is 'going wrong?' Holst & Miller-Morgan, (2021) made a broad inventory for the giant Pacific octopus (*Enteroctopus dofleini*), whereas Galante & Margulis (2022) narrowly watched spatial coordination behavior to figure out the strength of bonds in captive penguin (*Spheniscus humboldti)* pairs. Another place for making an ethogram is in teaching, it is useful for students to be confronted with an unusual animal and asked to think about what it is doing (see Wincheski et al. [2024] for *Octopus joubini* as a subject).

Cephalopods like the octopus come with some challenges for description, though. Three-fifths of the neurons are not in the brain but out in the arms, and the result is much peripheral control of the details of movement (Mather & Dickel, 2017). Grasso (2014) has suggested that the arm control system constitutes a plexus, an interacting set of similar neural units. This does not mean that the octopus has 'nine brains,' as has been suggested in social media, the brain does over-all coordination and planning though the arm ganglia control movement details. As well, the motor system is based on muscular hydrostats (Kier, 1988). Most molluscs have shells, onto which muscles attach and against which they move. Vertebrates have internal skeletons and arthropods external ones. Cephalopods have none, so for any action an arm designates some muscles to stiffen and other to move against them. Muscular hydrostats do have a constant volume, so an arm can be short and fat or long and narrow (Mather & Alupay, 2016). But it can also bend in any combination of two dimensions and twist clockwise and counter-clockwise, all of these at one location or all along its length. As there are eight arms, the possible action combinations seem almost infinite, though Kennedy et al. (2020) found there are more and less common arm actions; the vast majority were bending by the anterior arm pairs 1 and 2.

Such complexity seems almost to demand simplicity at its base, and Hochner (2013) believed he had found Motor Primitives such as Bend and Extend as arm movement basics. Recording arm position when an octopus reached up for a reward in a laboratory setting, he noticed bend propagation along the arm's length with articulation at specific points of the arm. But the stereotypy of action depended on the fixity of the situations, and when released from this constraint the octopus varied its action considerably. For instance, repeated Slaps at a menacing fish in the wild revealed variable combinations of bend and extend through repeats of the same action (Alupay et al, 2023). As well, closed loop visual feedback was used to aim anterior arms at the moving fish and posterior arms held to the substrate for stability. Mather (1998) identified a commonality when all arms were extended from the longitudinal plane of the body to make a two-dimensional flat surface, yet different alignments along this plane resulted in different postures, from Web-over to Flare to Retract. Still, there were constancies.

Do you have to do a lot of studying an animal to make an ethogram? Well, yes, and crowding in the lab distorts behavior; the *O. joubini* that formed a dominance hierarchy in confinement (Mather, 1980) were widely and randomly spaced in the field (Mather, 1982). It also can distort non-behavioral situations, see Calisi & Bentley (2009) for endocrinology. Behavior should be observed and tested in the wild, if possible. People tend to go off to inconvenient places for a natural setting, think of Jane Goodall's chimpanzees (*Pan troglodytes)* in Gombe, Africa, and Clutton-Brock's red deer (*Cervus elephas)* in highland Scotland. When you are there, animal subjects at first distrust you and hide from you, and marine animals can be particularly difficult to access. Howe et al. (2015) used spotting scopes to watch belugas (*Delphinapterus leucas)* at a distance and got only very general behavioral categories. Trueblood et al. (2015) used Remote Operating Vehicles to catalogue skin patterns in open-ocean *Dosidicus gigas* squid. Sukamoto et al. (2009) resorted to acceleration data loggers to at least get some information about what shag cormorants were doing during hunting dives. In contrast, Stanton et al. (2015) did a data base search and formed a meta-analysis for an ethogram of the Felidae—thorough, but not half so much fun.

Octopuses do not live anywhere near me (in Alberta, Canada) so I have to travel and no, they are not easy to watch, though I predominantly used snorkeling. In return, though, I went to watch in very nice places—Bermuda, Hawaii, the Caribbean, Moorea, Okinawa. My reasons for choosing those locations were simple ones, I took volunteers to help me watch and had to care about them too. We needed warm water. If you are floating stationary on the water so the animals will acclimate to you and forget you are there, you get really, really cold in around an hour, even with a good wet suit. Again, because these were volunteers, I used three categories of 'protected' in my choice of sites: politically protected and not susceptible to violence and chaos, ecologically protected without dangerous animals lurking nearby (the locals assured us the sharks in Moorea were no problem), and physically protected from major currents and waves smashing you onto rocks—leeward not windward shores.

Still, I did not start in the field but rather studied *O. joubini,* a small species (25 gm at maturity), in the lab. Small nocturnal animals are very difficult to study in the wild. I did my Master's studies watching and testing them and trying to figure out what they do with their lives (Mather, 1980). This included bringing one home; since *O. joubin*i is strictly nocturnal I could put my preschool children to bed, leave my long-suffering husband with a good book and just watch the octopus. I got very little publishable data from those two years, that is the trouble with basic research. Field researchers say that you will get nothing concrete out of your first field season, you have to learn what is there and what are interesting and possible questions to ask. But this is a problem in the modern fast-paced world of science, 'publish or perish' leaves little time for getting acquainted with an animal's normal life. Fortunately, there tends to be a small but constant supply of curious and idealistic students coming along to graduate studies.

There is another problem with starting from scratch to figure out what an animal is doing with its life. It is simple, banal, routine, no great discoveries or distinctive findings to get published in major journals, so funding agencies often do not see the point, and without money you cannot carry on research. I was lucky enough to be in Boston and discover an early variant of citizen science, called Earthwatch. I started out returning to my 'roots' and asking questions about what the same octopuses I studied were doing in the field, in the shallow sandy St. Joe Bay. It was conveniently a State Park so we and the Earthwatchers occupied several camping sites. I was trying to figure out if the octopuses were social, and no, it turned out that their distribution across the sand was controlled by whether they could find shells to hide in. It was a basic lesson, octopuses are vulnerable—no shells, no spines, no poison—and not getting eaten by a predator is so important that finding shelter controls their lives (Mather, 1982). So yes, I was gradually building up an idea of what an octopus was.

I am not sure what directed me to Bermuda for my next research site. Maybe it was Ron O'Dor, who wanted to tag and track octopuses, and it certainly helped that there was a research station with houses where volunteers could live. But I do remember that, when we visited there and looked out across the shallows wondering where to find an animal that is a master of disguise, a local shell collector told me that he looked for discarded clam and snail shells at octopus dens. To this day, I locate octopuses by their garbage heaps. Having a research team meant that we could follow a single animal in shifts and see what they were doing with their days. A volunteer would float a meter or two above an octopus, record what it was doing on an underwater slate for around an hour and be replaced by another, coming out in the hot sun to bask and warm up. It really was not a difficult life, and Ron's and my partners kept track of maintenance, food, and other daily living concerns. Finally, I could really focus on what the octopuses were doing and *vulgaris,* unlike the nocturnal *O. joubini*, had all the fabulous camouflage colours that I had only read about. In the end it resulted in five papers (e.g., Mather, 1991).

Are there lots of full, or even partial ethograms of cephalopods? No, animal behavior is heavily biased to mammals and sometimes birds. I did a quick search on Google Scholar and found the word ethology seldom used for studies on any invertebrate. Apart from cephalopods, Jan Leonard (Leonard & Lukowiak, 1986) is the only mollusc ethologist I found, and there are around 800 cephalopod species and at least 40,000 gastropods. Jan did one ethogram for the shell-less snail *Aplysia*, using it to point out to the physiologists who were already studying its reflexive behavior that they had some of it wrong. There were a couple of papers where Roger Hanlon's (1999) and Brad Seibel's groups (2015) used the word for evaluation of cephalopod skin displays. They are only part of the story of the animal's behavior, of course, but skin displays spread on a two-dimensional skin 'canvas' and are fairly easy to compartmentalize and specify. That line of research has continued up to today, although they tend to be an inventory of possible patterns in restricted areas, not of combinations linked to specific motivations. Anecdotal evidence can sometimes be useful to know what to look for, though Moynihan & Rodaniche's (1982) extensive descriptions of Caribbean reef squid *Sepioteuthis sepioidea* turned out to be fragmentary, confused and misleading for understanding their movement and displays. Sorting squid actions is difficult, too, in mid-water the squid has no substrate to act against, and is solely dependent on gravity (Mather et al., 2010). There is an especially nice assessment of squid patterning by Lin et al. (2017), but authors mostly don't use the word ethogram, instead this is referred to as repertoire. Fashions in wording change, but there are still some inventories, Crissy Huffard (2007) did a thorough description of behavior of the little tide-pool octopus *Abdopus aculeatus* and Gonzales-Navarette et al. have one coming up on *O. maya*. However, there are two approaches to the catalogue you make for an ethogram. One is functional: how does your species 'do' reproductive behavior, how does it feed, and so on. The other is physical: how does it move limbs, breathe, locomote. Most authors used the first, but my other background in human sensory-motor coordination meant that I focused on the physical approach.

I had conversations with my colleague Sergio Pellis (Pellis et al., 2014) about understanding movement, but the vertebrate-oriented movement assessment system that he used relied on limbs of fixed length and that did not work for octopus arms. But I persevered on describing octopus arm movement without that assistance, and then tried to get it published, a problem with descriptive research. Two major animal behavior journals turned it down flat, reviewers didn't think it was worth publishing. I tried *Journal of Comparative Psychology*, which is also about animal behavior though heavily into mammals and especially primates. I got two reviews back. One said "Fine, though fix the spelling mistake on page XX". The other said "Hurry up and accept this paper so I can use if for my class" (Mather, 1998). What a contrast, you just never know.

I kept chipping away at trying to understand octopuses, mostly lab work with Roland Anderson at the Seattle Aquarium, on problems of personality, looking at exploration and play, understanding their problem solving. We used different species, the medium sized *O. rubescens* and the giant Pacific octopus, *Enteroctopus dofleini.* But Roland was the one who tested them. I directed three graduate students looking at activity cycles, arm use and play, with *O. vulgaris* in Austria, but again in the lab. I got the chance to go back to the field when I got a small National Geographic grant to go to Hawaii to watch *O. cyanea*; I wanted to know how the risk of predation affected octopuses' hunting strategies and prey choice. We had an almost randomly assembled research group, and started by figuring out what the octopuses ate and where they lived--though that was not continuous watching, more like visiting. They ate crabs only, but the same species in other areas is much less selective and no, I have no idea why. We lived at first on the tiny Coconut Island, at the Hawaii Institute of Marine Biology. At the time it was fairly in disrepair, but field researchers are not picky about accommodation, and later we rented a house in town. We had one month of watching two octopuses in a confined pond on the side of the island, not enough animals to make conclusions about foraging pressures. Besides, when we introduced a moray eel (*Muraenidae)* predator, the octopus did not change foraging tactics or timing, so my prediction was wrong. Still there was a lifeguard platform on one side, used by Yarnall (1967) for the same purpose and left around for decades, so we got a lot of octopus watching in, and eventually published a paper on the Passing Cloud skin display (Mather & Mather, 2004) that was produced to startle crabs. Frame-by-frame analysis revealed that it 'moved' posterior to anterior and changed shape as it did so, but all this is *apparent movement* caused by sequential expansion and contraction of many, many chromatophores.

Maybe it was the popular book (Mather et al., 2010) that focused my thinking. A small local publisher mostly of gardening books, Timber Press, got in touch with Roland and asked him to write one. We had to go back to the basics about the daily lives of octopuses, Roland and I did alternate chapters, but the publishers did not like the two different 'voices' so I mostly wrote the second version. We had chapters with titles like Making a living, Not getting eaten, Sex at last. I had to summon my background information, read about others' work and put it all together, hopefully in a readable format.

Still, there had to be an opportunity to really focus on a repertoire. Khalil Iskarous from California got in touch with me, he wanted to study the actions of hydrostat movement systems—the human tongue, as he was a linguist, the roundworm and the octopus arm. The National Science Foundation had a special intersection grant between three areas: Animal Behavior; Perception, Cognition and Action; and Linguistics and this idea fit all of them. We had a post-doc, Jean Alupay, who had just finished studying *Abdopus,* and we decided to start with the ethogram that I did not really know I could do. You cannot just sit down and start to write, we had to build from what we knew and think about what we did not know. I had seen seven species: *O. joubini, O. vulgaris, O. rubescens, O. cyanea, E. dofleini, O. insularis* and *Eledone moschata*. I used to joke that while I was studying them, they had changed the genus in one (*O. dofleini* is now *Enteroctopus*), the species in another (the Bermuda species is now known to be *O. insularis*) and we are still quarrelling about *O. joubini* (it might instead be *mercatorius* but based on egg size). Although there are differences across the species in areas such as activity cycle and specific skin displays, their physical bodies were much the same so I felt that what actions they did would be similar across the Family. Thinking back to Hochner (2013) and Schleidt (1974), I felt we could start with the smallest units and build into combinations. How did they lift their head? Which arms did they walk with? What mantle postures could they take?

Jean and I worked out a rough draft, and then started to chip away at the uncertainties. Khalil found the money for her to go to several labs, watch and film what that particular species was doing and add a piece to the description. I only remember she went to the Gulf Specimen site back near where I got my Master's, in North Florida. I also remember realizing that conceptually spots, blotches, bars and stripes were actually extensions of a dot in different dimensions, and that these regularities were behind the many more elaborate skin patterns. There was a mini conference that year at the Seattle Aquarium, we presented our first draft there and asked for both feedback and film from other researchers there, which they generously provided. We built it bit by bit, often checking back and forth between the description, our memories and the pictures. It is surprising what you do not notice until you have to ask yourself. I would guess it took a full year, and this was from people who already had a good background.

Then we had to think about publication. Well, if *Journal of Comparative Psychology* liked Arms, maybe they would be receptive to an extension, a fairly complete ethogram. Jean filled it full of descriptive pictures, too. I have been in this business for decades, there are good and bad reviewers. I have a colleague who is well known in the area and also well known for suppressing the work of others in order to reduce the impact of rivals. Because rivalry in science is so strong, one can ask an editor to not send a paper to a particular reviewer. I am pretty sure that I asked and I am pretty sure that the editor sent it to him anyway, though I will never know. The other two reviewers sent a mixed bag of mostly helpful suggestions. Reviewer 1 sent 50 comments, nearly all of them negative, though they were all answerable. I vividly remember one comment about how the flexible octopus siphon tube, used for exhaling and also jetting water at things, closed off. The tip folds inward, we had checked. "You are wrong" he said. No, sorry—we looked. Anyway, that is part of the game, we patiently answered him and in a few cases changed wordings. The editor sent the corrections for re-review and must have sent back to Reviewer 1, because we received a further 30 criticisms, and appended to this feedback was "I don't want this to be published." It must have been apparent to the editor that *we* were not the problem, he said to us "If you answer all these corrections, I'll publish it," and they did (Mather & Alupay, 2016).

What did we learn, and what can we pass on, from doing it? We did find the regularities that Drummond (1981) suggested were there in behavior. Maybe it is construction by humans to form gestalts as 'natural units,' but despite the muscular hydrostat system and the distributed control, smaller units did combine into larger ones to produce organized behavior. The octopuses knew what they were doing and we just followed them and found out, others can do the same with equally different animals.

Still, I feel like someone at the festival in Thailand where they release lights in paper bags to float down the river. We seldom know the effect of our papers on other researchers. It's gone, we did our best, I hope it helps.

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