Observation on Mating of the Giant Pacific Octopuses

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Abstract
While there are documented observations on mating of many octopus species, there are relatively few of each species and fewer still observations *in situ*. Because different octopus species may be flexible in their courtship and mating positions, such observations are valuable for comparative studies. We present here observations on mating of the giant Pacific octopus *Enteroctopus dofleini*, both *in situ* and in public aquariums. The males used "mounted mating" or "distance mating," using their hectocotilized arms to pass spermatophores. Such flexibility on the part of the male may be advantageous, depending on the females' positions and postures. Matings took a relatively long time, a mean of 245 min (S.D. = 39). There were commonalities in body patterns during mating in both males and females. Males were papillose and mottled reddish brown in color with frontal and mantle white spots visible while females were smooth and generally paler than the males. We suggest that observations of octopus matings should include location, habitat, species, size, relative maturity, position, posture, body patterning and its changes, possible courtship or male display routines, contextual variables about courtship, mating duration, respiration rate, and presence or absence of the arch and pump spermatophore transfers. These criteria are presented so observers can make appropriate comparisons between species.

Introduction
The general method by which octopuses mate has been known for millennia. Aristotle stated "the male octopus has sort of a penis on one of his tentacles ... which it admits into the nostril of the female" (translation by Peck 1970). While deficient in accurate details, his description was remarkable for his time and essentially correct. Despite this long history, octopus mating behavior has been meticulously reported in relatively few species and from fewer yet in the wild. Wells and Wells (1972) reported about mating: "Any information ... and particularly any information gathered from observations in the wild, is of greatest interest." Such intraspecific observations are important to determine species commonalities and differences.

As a general method, octopuses use a modified or "hectocotylized" arm in mating but it does not function as a mammalian penis as Aristotle thought. During mating, spermatophores are released from the terminal organ of the male's reproductive tract (commonly called a penis) and are passed into a groove in the male's third right arm (Mangold 1987). The end of this hectocotylized arm is modified into a copulatory organ (ligula) for transferring spermatophores into the oviducts of a female during mating, and it might also be used to remove sperm from previous matings by different males (Hanlon and Messenger 1996). During actual spermatophoric transfer, the male passes the spermatophore using an "Arch and Pump" action, first described in the European common octopus *Octopus vulgaris* by Wells and Wells (1972)

During mating, octopuses may employ either of two general positions, either male on top ("mounted mating") or side-by side ("distance mating" - *sensu* Hanlon and Messenger 1996). During distance mating, the hectocotylized arm is extended some distance to reach the female (1963; Mangold 1987). Hanlon and Messenger (1996) classify a number of octopus species according to whether they use mounted and distance mating. Some species can use both methods. Mather (1978) found that the Caribbean pygmy octopus *Octopus joubini* used mounted mating in the laboratory and used distance mating in a well-spaced semi-natural situation.

Of approximately 150 octopod species (Norman 2000), rigorous observations of mating have only been reported in a few species, summarized in Mangold (1987), Hanlon and Messenger (1996), and Norman (2000). The dearth of mating observations among otherwise well-known octopuses is exemplified by the giant Pacific octopus *Enteroctopus dofleini* (formerly *Octopus dofleini*, see Hochberg 1998). There are only two brief descriptions of matings by giant

Pacific octopuses in the literature, both in captivity (Gabe 1975; Mann 1984). No observations of its mating have been documented from the wild (the citation of such an observation in Hanlon and Messenger (1996) is erroneous). Gabe (1975) reported that the male mounted the female and the mating lasted 4 h, during which two spermatophores were passed into the female. Neither Gabe (1975) nor Mann (1984) gave any indication of the arch-and-pump spermatophoric transfer (Wells and Wells 1972; Wodinsky 1973) in giant Pacific octopuses. Mather (1993) suggested that observations of such octopus matings in captivity might be influenced by unnatural conditions of crowding and sudden contact. To clarify how giant Pacific octopuses mate under different conditions, we present further observations of their matings, both in the wild and in captivity.

Observations

Observation #1
Date: 11 November 1998
Time: 1000
Location: Wain Rock, Saanich Inlet, British Columbia, Canada
Depth: 13 m
Water Temperature: 10.2^0 C
A female giant Pacific octopus was in a large den formed by the junction of three large rocks at the base of an underwater cliff. A medium-sized male (estimated weight 25 to 30 kg) was resting on the rocky substrate approximately 1 meter away from the den. There was no physical contact between the octopuses at this time. On a subsequent dive 3 hr later, the male was observed at the same place in the same position. He was a medium reddish-brown color and his skin was papillose. Two mantle white spots and one frontal white spot were clearly visible. The male was facing the den with his dorsal arms in contact with the rock around the entrance to the female's den. Careful examination showed that the third right arm was now extended into the den. The female was a normal, smooth reddish color with no papillation or white spots. Approximately 15 min of observation showed no change in the color, skin texture, respiration or body position of the octopuses. No arch and pump was observed. Due to the constraints of depth and nitrogen load from the previous dive, the divers were then forced to leave.

Observation # 2
Date: 14 March 2001
Time: 1400
Location: Port Washington Narrows, Puget Sound, Washington State
Depth: 10 m
Water Temperature: 8.2^0 C
A pair of octopuses was found together at least 3 m from any shelter. The animals appeared equal in size (estimated at 15 kg); both were facing the same direction with the male gripping the mantle of the female with his dorsal arms. The male was densely papillose and dark reddish-brown with white frontal and mantle spots visible. The female was a much paler orange-yellow and her papillae were erect only at the base of the arms. At one point the female exhaled strongly and ejected a piece of spermatophore (approximately 2 cm long) from her siphon. The ends of two intact spermatophores were visible on the substrate beneath the pair trailing out of the mantle of the female. The female appeared to be disturbed by a camera flash and tried to move away, causing her mantle to be greatly elongated as the male remained firmly anchored to both her body and the substrate. No arch and pump was observed. They remained attached together for 10 min of observation.

Observation 3
Date: 17 January 2001
Time: 1205
Location: The Seattle Aquarium, Seattle, Washington State
Water temperature: 9.7^0 C
A female was placed in a 12,000 l display tank and the male was added 10 min later. The female weighed 18 kg and the male weighed 20 kg. The female was sitting motionless in a lower corner of the tank when the male was added. She was oriented horizontally, facing outward from the corner. As he swam to the bottom, the male inked. He jetted directly to the female and enveloped her with his web and arms. There was then an active intertwining of arms for 2 min. At the end of this period, the female was facing into the corner and the male was on top of her facing the same direction, with his dorsal arms wrapped around her head and mantle. The hectocotylized arm of the male was inserted into the right mantle opening of the female. He was a mottled gray/pink color with frontal and mantle white spots apparent. The mantle was papillose. The female was dull red and smooth. The male's respiration rate was 5.9 sec/breath, and the volume was judged "deep breathing."

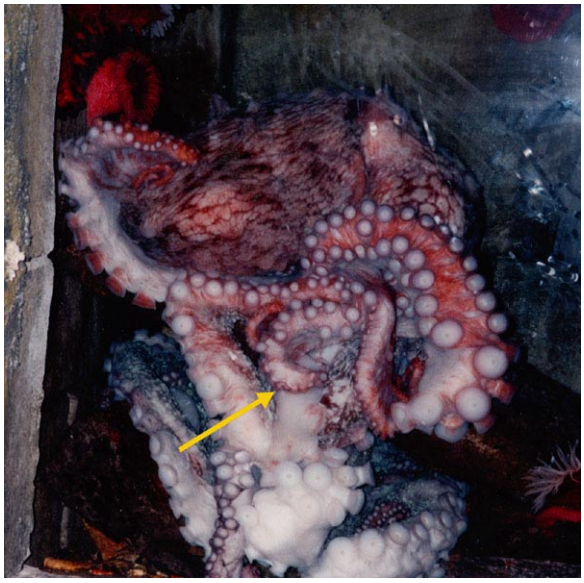

Figure 1. A male and female giant Pacific octopus mating in captivity at the Aquarium of the Bay (San Francisco, California, USA). The male is on top. The arrow points to the insertion of the male's hectocotylized arm into the mantle cavity of the female. (Photo by Kevin O. Lewand.)

At 78 min after first contact, there was an increase in the intensity of the mottling and the brightness of the white spots on the mantle of the male as he raised his body up off the female slightly and then settled onto her again, whereupon the intensity of the mottling and white spots dulled. This was likely an arch and pump. At 3 hr 43 min, the male removed the hectocotylized arm. He moved away from the female at 4 hr 1 min. At this point, he was smooth and bright red; she was smooth light pink.

After 17 min apart at the opposite corner of the tank, the male again approached the female. She was in the same corner facing outward. He mounted and grasped her as before and turned mottled and papillose with mantle and frontal white spots apparent. After 3 min, she turned toward the corner as before, so they were facing the same direction. He again held her with his dorsal arms. His hectocotylized arm was inserted into the mantle of the female. They maintained this position for another 4 hr 12 min. He then moved off to an opposite corner of the tank and turned smooth dark red. She maintained a smooth pale pink for several minutes and then turned mottled and papillose. No spermatophores were observed protruding from the female's mantle cavity as reported by Mann, Martin and Thiebsch, (1970).

Observation 4
Date: 15 April 1999
Time: 0900
Location: Aquarium of the Bay, San Francisco, California
Water Temperature: 10.0^0 C
At the Aquarium of the Bay, a male was added to a female's tank. He crawled to her and there was intertwining of arms for 10 min. At the end of this period, the female retreated into her rock den and the male sat on top of it. The male's hectocotylized arm was observed to extend into the female's right mantle opening (see Figure 1). The female was smooth and pale, the male mottled and papillose. They maintained this position for 4 hr 50 min. Both remained in the tank and three days later mating was observed again in exactly the same position. The second mating lasted 3 hr 15 min. No arch and pump was observed during either mating.

Observation #5
Date: 10 November 2002
Time: 1130
Location: Wain Rock, Saanich Inlet, British Columbia, Canada
Depth: 18 m
Water Temperature: 10.3^0 C
This is the same den as described in Observation #1. The den formed by the junction of three large rocks at the base of an underwater cliff. In this observation the male (estimated weight 20 to 25 kg) was wedged into a crack behind one of the large rocks forming the den and was approximately 1 meter away from the den. When discovered, the male appeared dark but was seen to be a pale brown under the divers' lights. The skin was papillose but not strongly so. Within seconds of discovery, the male moved out of the crack, flushed a red colour while the skin flattened and the male made a definite move towards the divers. The frontal white spots were not observed but as things were happening very quickly they may have been overlooked. It was confirmed at this point that the octopus was a male. As the divers retreated, the male returned to the crack in the rock and resumed his former position and color. The divers then moved to the den and examined the interior to discover a second octopus presumed to be female. This octopus was positioned facing the male with her right side visible. Her weight was estimated at 15 to 18 kg and her colour was slightly redder than the male but not the normal red of resting animals. Her skin was also moderately papillose. There was strong, continuous physical contact between the octopuses at this time, but the divers were unable to see if the hectocotylous was inside the female mantle cavity. It was not seen on the female's right side. On a subsequent dive 2 weeks later the den was seen to be walled off and an octopus was present. There was no midden heap. A week later (November 20, 2002) the female was observed on the roof of the den in the egg laying position.

Observation #6
Date: 23 November 2002
Time: 1200
Location: Wain Rock, Saanich Inlet, British Columbia, Canada
Depth: 20 m
Water Temperature: 10.0^0 C
The den is under a single large rock measuring 2.3 meters long by 1.2 meters wide. In 1999 a female giant Pacific octopus was seen to lay eggs and successful raise them to hatching in this den. In this observation two octopuses were discovered in the den facing each other and in contact with each other but mating could not be confirmed. Estimated weight was 18 to 20 kg and it was not possible to tell the male from the female. Both animals were a pale brown with darker stripes down the length of the mantle and extending down onto the shoulders of the arms. Both animals were moderately papillose. The position of the animals made the observation of frontal white spots difficult.

Divers also discovered a second male in a known den approximately 4 meters away from the mating pair. When discovered, the male came out of the den and moved after the diver, with arms fully extended, up into the water column for a distance of approximately 3 meters. It was clear that both R1 and L1 had been amputated with R1 having regenerated about 8 cm. L1 was still a stump with no sign of regeneration. Weight was estimated at 18 kg. As the diver retreated, the octopus returned to the bottom and moved up the slope towards the den with the pair. At this point, the approaching male was a darker reddish-brown and strongly papillose. As the male approached the den on one side, one of the pair in the den moved out of the entrance of the den on the other side to observe the divers. The new male turned a pale brown colour and reached in the entrance nearest him. Almost immediately he withdrew his arm and flushed a darker red. The animal watching the divers withdrew back into the den very quickly as the male on the far side retreated. The second male now moved around the top of the rock and approached the second entrance and reached in. His color had gone from dark to pale brown and the skin was lightly papillose. Again, the male withdrew at contact and his skin darkened and flattened. He moved away from the den and again pursued a diver up into the water column for several meters before settling back to the bottom and returning to the den he had come out of. Elapsed time was 5 to 7 minutes.

An inspection of the pair in the den showed that they were now sitting side by side and were facing the entrances to the den. Their color was again a pale brown and the skin was lightly papillose.

Discussion

The variable conditions (wild vs. captive; distance vs. mounted) and often limited observation times of these matings so far prevent a thorough description of the mating in the wild of giant Pacific octopuses. Nevertheless, there are a few features consistent to the observed matings. Males were darker than females and were generally a dark reddish brown in color. They typically displayed frontal and mantle white spots while the females did not. Skin texture also varied with sex; males were conspicuously papillose while females remained relatively smooth. The color photograph of mating of giant Pacific octopuses in captivity in Mann (1984) confirms these observations. It is interesting that these body patterns are consistent, regardless of the surroundings, and that the octopuses did not camouflage appropriately.

These observations on mating confirm those of Mather (1978), that mating positions may not be species specific. Some octopus species may mate either at a distance or in the mounted position, depending on their setting. Mather (1978) suggested that Caribbean pygmy octopuses used mounted mating in captivity and distance mating in the wild. Our observations show that in giant Pacific octopuses both methods are used in both settings. Such flexibility is obviously adaptive for a male octopus. When females are encountered in the open while they are foraging, mounted mating may be necessary. If a female is found in a den, the male may need to use distance mating to get at a female deep in a narrow den where he cannot mount her. Strictly speaking, since the male is usually the "active partner," he probably must do what he can to ensure contact is maintained. However, we must remember that a female must be receptive to a male for an actual mating to take place and actually may be the active partner in some species (Mangold 1987).

These observations of octopus matings in the wild are incomplete. A complete mating, including possible courtship or male displays, is unlikely to be observed in the near future due to the short period of time divers can spend in cold North Pacific waters. Future use of ROVs and submersibles may further these observations. Until that time, it is unlikely we will be able to observe possible courtship in this species *in situ*.

The duration of copulation is longer in giant Pacific octopuses than that of most other octopuses (see table in Hanlon and Messenger 1996). Averaging our mating durations with that of Gabe (1975) gives a mean of 256 min. Only the common Sydney octopus *Octopus tetricus* at 360 min has been reported to take longer (Joll 1976). Why would this species need such a long time to complete mating? First, it may be because it lives in cold water and all life processes of poikilotherms are slowed in colder water. However, the spoonarm octopus *Bathypolypus arcticus*, which lives in 2-3^{0}C water, mates in just 3 min (Wood 1998), so this may not be the answer. Secondly, as befitting the world's largest octopus species (High 1976), it has the largest octopus spermatophore at over 1 m (Mann *et al.* 1970). Male giant Pacific octopuses only produce about 10 spermatophores, each containing about 37 billion sperm (ibid.). The release and placement of such large, limited, and genetically valuable resources are highly critical and may need careful placement taking much time. A third reason an octopus mating may take a long time is suggested by Hanlon and Messenger (1996): to possibly eliminate sperm competition. They suggest the tip of the ligula in octopuses is spoon-shaped to remove other males' sperm already present in the female's oviducal gland. Such a process (if present) may be time consuming.

Mather (1993) pointed out that octopus mating is much more than "mere copulation" and that observation should include other factors. There are differences between species in such factors as position, body patterns, courtship, and male displays. Observations of matings need a certain rigor for comparisons between species. At a minimum, we suggest that observers note location, habitat, species, size, relative maturity, position, posture, body patterning and its changes, habitat, possible courtship or display, contextual variables about possible courtship, mating duration, respiration rate, and presence or absence and number of the arch-and-pump spermatophore transfers (Wells and Wells 1972; Wodinsky 1973). The paucity of documented mating observations in the world's largest octopus species and the one most exhibited by public aquariums (Carlson and Delbeek 1999) indicate the usefulness of such further observations, especially in the field.

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