Title: Playtime for Cephalopods: Understanding the Significance of Play Behavior in Octopus bimaculoides

Katarina Jarmoluk[1] and Galit Pelled[1,2,3+]

1. Department of Mechanical Engineering, Michigan State University, East Lansing, MI, United States
2. Department of Radiology, Michigan State University, East Lansing, MI, United States
3. Neuroscience program, Michigan State University, East Lansing, MI, United States

+ Corresponding Author: Galit Pelled, Ph.D.

pelledga@msu.edu

(517) 884-7464

Professor, Mechanical Engineering, Radiology, and Neuroscience

Michigan State University

775 Woodlot Dr. East Lansing, MI 48824

Key Words: Octopus, behavior, welfare, cognition, behavioral analysis

Abstract: (200 words)

Play is considered to be an essential part of development that supports learning, memory, and the development of flexible behavioral strategies. An increasing amount of non-mammalian species have been discovered to engage in play behavior, but there has been little research into play behavior in cephalopods specifically. Here we studied play behavior of wild-caught, laboratory-housed California Two-Spot Octopuses, *Octopus bimaculoides.* The behavior observed in these animals is consistent with established criteria of play behavior in animals. The evidence of play in *O. bimaculoides* provides further insight into the evolutionary development of play behavior as a whole, the characteristics of play in an under-studied species, and also has the potential to be used as a factor in determining the welfare state of octopuses to improve their management in captivity.

Background:

Play is considered to be an essential part of development, as it is known to engage neurobiology mechanisms supporting learning, memory and the development of flexible behavioral strategies. Play is also important in adulthood, and human and animal research suggests that playful behavior and internal motivation is linked to mental health (1).

When play behavior first started growing in popularity as an important field of scientific study, the only non-human animals thought to be capable of play were other mammals and possibly birds (2, 3); evidence of play behavior in other species such as reptiles or fish was often discredited quickly and without sufficient evidence to disprove it. One example of this is when the naturalist Charles Holder described needlefishes that would jump over logs as being a potential play behavior (4-6), which was promptly dismissed by ethologist Frank A. Beach (3) as a method of parasite removal despite having no evidence to support this counterargument (7). Over the past few decades there has been growing appreciation of the importance of play in development, socialization and communication, as well as an increasing amount of evidence showing that play behavior is also found in reptiles (8, 9), fish (9-11), and even insects (12).

Octopods are soft-bodied marine mollusks of over 300 known species within the class Cephalopoda, containing two major groups: the finless incirrate octopuses and the finned cirrate octopuses. Within the category of incirrate octopuses is the family Octopodidae, which contains the majority of octopods at over 200 species. Octopodidae are benthic creatures and are characterized by their eight arms, each possessing one to two rows of suckers (13). The majority of an octopus' neurons are located within the arms (14, 15), giving it a decentralized nervous system where the arms are capable of making semi-autonomous decisions and can engage in grasping and foraging behaviors even after being completely severed from the rest of the body (16, 17). They are also capable of changing the color and texture of their skin, which they commonly use as a method of camouflage or startle display (18).

With their large brains, unique nervous system, and wide behavioral repertoire, octopuses are ideal models in a broad variety of fields and subjects, including aquaculture, neurobiology, climate change, and more (19). In particular, they are becoming increasingly common as a model in biomedical and neuroscience fields, as well as in robotics (17, 20-26).

The discussion of play in octopuses is not a new occurrence. Play or play-like behaviors have been observed and recorded in a few species – the common octopus, *Octopus vulgaris* (27), the Giant Pacific Octopuses, *Octopus dofleini* (28) – and it has been anecdotally described in regards to the Caribbean Reef Octopus, *Octopus briareus* (29) and more recently in the California Two-Spot Octopus, *Octopus bimaculoides* (30). *O. bimaculoides* (Pickford and McConnaughey, 1949) is a species endemic to the coasts of California and Mexico's Baja Peninsula. It is becoming popular in biomedical research due to several biological and husbandry reasons (26). First, it is found off the coast of southern California and is readily available through suppliers. Second, unlike another studied octopus, *O. vulgaris*, *O. bimaculoides* was determined to be one of the least likely octopus species to attempt to escape in captivity (31). It is a large-egged species that is tolerant of crowding, with benthic hatchlings that display adult-like behaviors almost immediately, making it an ideal candidate for culture within the laboratory (32, 33). A third reason for the growing interest in using *O. bimaculoides* in the laboratory is the publication of its genome (34). Therefore, it would be important to characterize the behavior of this specific species.

The presence of play behavior in octopuses also provides valuable insight into the origins of play behavior itself. The majority of evidence for play behavior originates from placental mammals, a group which at approximately 4300 species makes up only a small fraction of the roughly one to two million species of animals currently present on earth (35). The existence of play in octopuses, such an evolutionarily distinct species from eutherian mammals, provides evidence against the notion that play is evolutionarily homologous. As described by Burghardt, if the play behavior thus far seen in octopuses does constitute valid play, then the development of the biological ability to evolve and perform playful acts dates back to over a billion years (10).

Burghardt's (10) five criteria were used to determine whether observed behaviors constituted as play. Briefly, these criteria are as follows: 1) there is no immediate function to the behavior in the context in which it is performed; 2) the behavior is voluntary, spontaneous, or autotelic (done for its own sake); 3) there is a structural or temporal difference from other typical behavior; 4) the behavior is repeated but not stereotyped; and 5) the animal is healthy and free of stress and competition.

In addition to the importance of understanding octopus play in regards to the evolutionary development of play behavior as a whole, it may also be valuable in terms of assessing an animal's welfare state. It is well-understood that an animal's welfare state affects the quality of scientific research. An animal's body is affected by its state of mind (36). Inadequate welfare can cause abnormal behavior, physiology, and immunology (37). It has been concluded that the most important measure for ensuring the protection of cephalopod welfare in both laboratory and field settings is the refinement of methods of maintenance, care, and culture (38, 39). According to Sykes & Gestal (40), "The practice of good (positive) or bad (negative) welfare in [cephalopod] research, maintenance, rearing or culture conditions will determine the existence of pathologies."

There is existing research that shows that stress negatively affects *O. bimaculoides* physiology and behavior (41, 42) and may be related to stereotypic behaviors such as autophagy (43). For captive cephalopods, enrichment is an important management tool that can be used to overcome the inherent stress of being held in captivity (44). Ahloy-Dallaire et. al. (45) suggested that there is a consistent relationship between animal welfare and most types of play. Evidence suggests that positive affect increases play and negative affect can significantly suppress many types of play, both in animals and humans. The term 'affect,' according to Mendl and Michael (46) is used to describe valent (positive or negative) states including emotions, moods, and other

valanced components of sensation. Since there have been very few deliberate records and measurements of octopus play behavior, the association between play and welfare in the Octopodidae family remains to be determined. Nevertheless, it is likely that an octopus with a negative affective state would display reduced play behavior, or an absence of it altogether.

Methods:

All procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University. Adult *O. bimaculoides* were obtained off the coast of southern California. Tank and environment set-up and protocols were described in detail by VanBuren et. al. (26). Octopuses were housed separately in the lab for up to 5 months. Octopus welfare was regularly assessed using a version of the Giant Pacific Octopus health and welfare assessment tool developed by Holst and Miller-Morgan (47) that was modified in order to be appropriate for *O. bimaculoides*.

To monitor the octopuses, Wyze Cam V2 and V3 cameras were set up facing the front of each tank containing an octopus. Cameras were set either to record continuously, or to record only motion activities. The cameras automatically saved all motion events to micro-SD cards, and in addition, the Wyze phone app allowed for a live view of the cameras and the ability to manually record this live video to the phone using a start/stop recording function. Videos taken with portable video cameras were also analyzed.

Octopuses were fed crabs twice a day and shrimps approximately twice a week. Initially when shrimp was fed, it was simply placed into the tank with the octopus using a pair of forceps. If the octopus did not show immediate interest, the shrimp would be moved around the tank with the forceps to simulate the motion of live prey. Putting the shrimp in a closed test tube was introduced in an effort to increase mental stimulation and increase the duration of a mimicry of the octopus' natural foraging and hunting behavior.

In order to train the octopuses to open the test tube by unscrewing the cap, a step-by-step process was used where the first exposure to the test tube containing the shrimp was without the lid on. If the octopuses removed the shrimp from the uncapped test tube successfully, then for the next shrimp feeding the cap would be screwed on loosely so that it could be opened in about a quarter turn. As the octopuses succeeded in opening the loosely capped tube to access the shrimp, the cap would be gradually tightened in subsequent feedings to increase the difficulty of opening it. This process of increasing tightness continued with each feeding until the octopuses could remove a cap that was fully screwed on.

Results:

Three octopuses engaged in object play with the plastic test tube cap. Two of the octopuses were only observed playing after they had unscrewed the cap and consumed the shrimp within, while the third octopus engaged in object play almost immediately after it had grasped the shrimp in its arms and brought it to its beak. Notably, none of the octopuses chose to play with the test tube itself despite its similar floating properties. For all three octopuses, play consisted of the octopus releasing the cap from its grasp so that it floated upwards into the water

current of the tank. As it began to float past, the octopus would reach out to grab it again, pull it in closer to its body, then release it again. This cycle of grabbing and releasing would be repeated several times, with the duration of the cycles varying in length. The number of cycles that were repeated before the octopus stopped engaging with the cap was also variable. A video capturing octopus's play can be found in Supplementary Data (Video 1).

During play, the octopuses showed a variety of skin coloring and patterns. One octopus (Figure 1) typically had an "acute mottle" pattern, characterized by bright blue or flashing ocelli, yellow-orange spots, integumental trellis, and a rounded mantle (18, 33). Another octopus played while in a uniform pale brown phase, although it did at times display a flashing ocelli pattern similar to that of the octopus in Figure 1. This flashing ocelli pattern was typically otherwise seen when the octopuses were hunting or consuming food. These octopuses did not show any major stress behaviors (such as stereotypies, reclusiveness, or inking or defecation provoked by the presence of a caretaker) either during play or outside of it.

The location within the tank that the octopus would play also varied. The octopus that played the most times typically would bring the shrimp with it back into its den, made up of a hollow ceramic "rock" with one opening. It would then orient itself so that it was facing outwards at the opening of the den and remain within the den for the duration of play unless the cap floated out of reach, in which case it would either stop playing or leave the den to grab it again. The other two octopuses both played outside of their dens, in the same general area of the tank where they had unscrewed the cap of the test tube.

The arms used to grasp and release the test tube cap were primarily the first two arms on either side (R1, L1, R2, L2). In some cases, such as when an octopus was using those arms to hold onto the test tube still, other arms were used (R3 and R4). In all octopuses, at least two of the rear arms were used as an anchoring point to a surface in the tank during play, most often the gravel bottom but sometimes to live rock or the inside of an artificial rock den.

Octopus ID	Sex	Number of Times Observed Playing	Arms Used
A	M	1	L1, L2, R1, R2
B	M	7	L1, L2, L3, R1, R2, R3
C	M	2	L1, R1, R2, R3, R4

Table 1. Characteristics of Play Behavior in Individual Octopuses

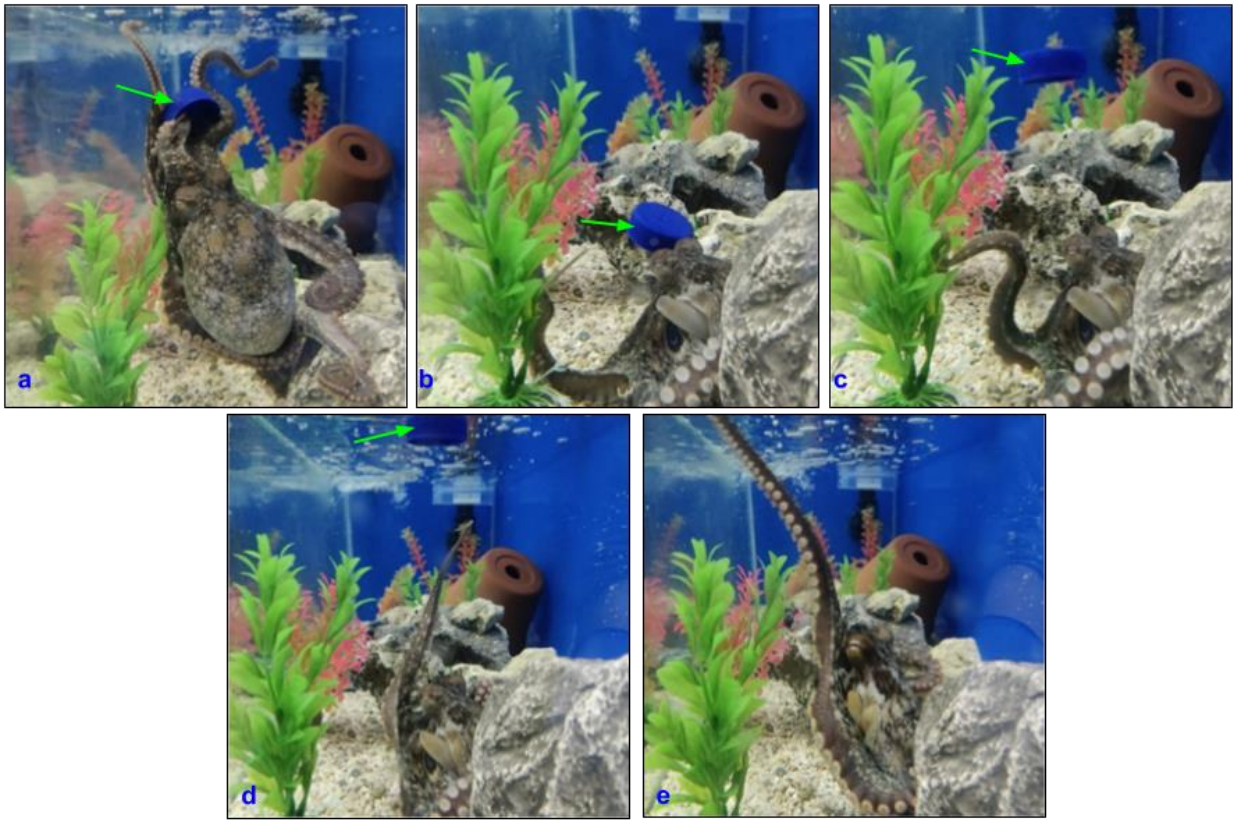

Figure 1. Octopus playing with a plastic cap. An *O. bimaculoides* grabs a test tube cap with its arms (a), pulls the cap towards itself (b), then releases it into the tank current (c) and reaches to grab it again as it moves away (d, e). The blue cap is indicated by a green arrow in pictures a-d, and is not visible in picture e, after being pushed away by the tank current. This sequence was typically repeated upwards of 5 times and was observed in this individual octopus on several different occasions throughout the four months it was housed in the lab.

Discussion

Notably, the discovery of play behavior of the animals reported here was incidental since these animals were being used for biomedical research purposes. However, all of the octopuses within the lab were approximately the same age and were all housed under the same environmental conditions. This did provide some measure of a controllable and reproducible setup and conditions. Burghardt (10) also provides justifications for using anecdotal evidence in ethology, and notes that the benefit of anecdotal evidence particularly applies to species that are lacking in-depth ethological study – such as *O. bimaculoides*. In addition, quantitative analysis of collections of anecdotal evidence of play in non-human animals indicates that it is possible to document phylogenetic trends and differences across species by use of informal observations of scientists (Whiten and Byrne, 1988).

While there were eight octopuses in total housed in the laboratory during this time period, only three of them were observed displaying play behavior. This does not necessarily mean that none of the other five octopuses engaged in play, as most of the animals were not constantly

recorded. In addition, instances in which the octopuses moved slowly or were towards the rear of the tank were not consistently captured and recorded by the Wyze camera motion sensors. There are many factors that may have also contributed to the occurrence of play in individual octopuses, such as life stage (particularly regarding senescence), sex, or even personality. Although most octopuses did not learn to completely unscrew a test tube cap, which was necessary in order for them to have access to the free-floating cap, all octopuses were presented with other objects in attempts at enrichment, such as Legos, plastic aquarium plants, seashells, and a plastic "foot toy" designed for parrots.

Mather and Anderson (48) determined that octopuses (*Octopus rubescens*) have individual personalities, characterized by three factors: activity, reactivity, and avoidance. These personality traits may influence the likelihood of an octopus to engage in play activity. The octopuses that displayed play behavior were often active during daytime hours and sought to engage handlers during daily tank maintenance. Comparatively, the octopuses that frequently withdrew from handlers and remained in their dens did not show any signs of play behavior. There is a possibility that the difference in personality between the octopuses housed in the lab could have influenced the likelihood of an individual octopus both to learn how to open the test tube, and to engage in object play with the plastic cap.

In order to determine whether a behavior was play, Burghardt's criteria for play (10, 49) were used and are addressed. First, the behavior does not have an immediate function in the context in which it is performed, and second, it is voluntary, spontaneous, or autotelic; In our report, although the opening of the test tube by removing the cap was a behavior that was intentionally taught to the octopuses, any form of interaction with the test tube cap beyond that was self-motivated. Octopuses were rewarded for opening the test tube immediately upon successful removal of the cap by being able to access the piece of shrimp. If an hour had passed and the octopus had not opened the tube, a caretaker would then remove the cap and return the opened test tube, without the cap, to the octopus. This meant that the only behavior the octopus was given a reward for was the opening of the test tube itself – any continued engagement with either the test tube or the cap was motivated internally, without the expectation of further reward. Thus, it is unlikely that the behavior was food-motivated.

If the behavior was not done to achieve a food reward, another possible motivation could have been to gain the attention of the caretaker. There were several times in which the behavior occurred while the caretaker was in the vicinity. However, the behavior also occurred on multiple occasions when the caretaker was no longer present. Had the goal of the behavior been to receive some form of engagement from the handler, it would not have been performed in their absence. Both of these factors suggest that the behavior was autotelic, as it provided no benefit to the octopus other than whatever pleasure it may have received through playing with the object.

Third, there is a structural or temporal difference from other typical behavior; In our study, the motion of the arm made when the octopus reached out to grab the test tube and pull it towards itself was also seen on other occasions – typically at any other instance where the octopus attempted to grab something that was not in its immediate reach, such as when reaching for any food source that was not moving on its own (when catching live fiddler crabs, octopuses typically engaged in the hunting tactics used to catch crabs that were described by Bidel et. al. (50)). However, the repetition and the time spent engaging with the test tube cap made this behavior markedly different from other behaviors with clear motivational causes.

Fourth, the behavior is repeated but not stereotyped; Two of the three octopuses in this study displayed this behavior on more than one occasion. Stereotypic behavior is characterized by its rigidity and repetition (51). The octopuses only engaged in this behavior intermittently, not every single time they were presented with the shrimp in a test tube. If this behavior were stereotypical, it would have been expected to be much more consistent in terms of duration and physicality. However, the octopuses that each performed this behavior multiple times showed variation in the duration of play, which arms they played with, where in the tank they played, and how many cycles of play they completed. This suggests a level of flexibility to the play behavior, which is counter-indicative of stereotyped behavior. In addition, play only occurred after the octopuses had been familiarized with the test tube and cap. This is consistent with the suggestion that play is preceded by exploration (52).

Finally, the animal is healthy and free from stress and competition; The octopuses housed in our laboratory were regularly assessed using a modified welfare assessment scheme as described in the methods section. The octopuses that engaged in play or play-like behavior had been concluded to be in positive welfare states during the time period that play occurred. Play behavior did not occur until after the octopus had acclimated to the laboratory environment and its caretakers.

In conclusion, the behavior of the O. bimaculoides reported here was consistent with previously established criteria for play and provides increased evidence for the existence of play in octopuses, which have a nervous system and evolutionary history that is quite separate from that of mammals. This supports the theory that play behavior evolved in multiple separate instances in history, as opposed to having developed at one singular point in time, and that play is a conserved behavior across species that may play a crucial role in development, but may also be important to an animal's well-being in adulthood.

Acknowledgments: The authors would like to acknowledge financial support from the NIH: UF1NS115817.

1. Blois-Heulin C, Rochais C, Camus S, Fureix C, Lemasson A, Lunel C, et al. Animal Welfare: Could Adult Play be a False Friend? 2015;2(2):156-85.

2. Fagen R. Animal play behavior. Oxford, England: Oxford University Press; 1981. 684 p.

3. Beach FA. Current Concepts of Play in Animals. The American Naturalist. 1945;79(785):523-41.

4. Holder CF. Along the Florida reef. New York: D. Appleton and company; 1892.

5. Holder CF. Stories of animal life. New York: American Book Co; 1899. Available from: http://books.google.com/books?id=MHxEAQAAIAAJ.

6. Holder CF. Why and How Fishes Leap. Scientific American. 1903;88(9):151-2.

7. Burghardt GM. Play in fishes, frogs and reptiles. Current Biology. 2015;25(1):R9-R10.

8. Barabanov V, Gulimova V, Berdiev R, Saveliev S. Object play in thick-toed geckos during a space experiment. Journal of Ethology. 2015;33(2):109-15.

9. Dinets V. Play behavior in ectothermic vertebrates. Neuroscience & Biobehavioral Reviews. 2023;155:105428.

10. Burghardt G. The Genesis of Animal Play: Testing the Limits2005.

11. Burghardt GM, Dinets V, Murphy JB. Highly Repetitive Object Play in a Cichlid Fish (Tropheus duboisi). Ethology. 2015;121(1):38-44.

12. Dapporto L, Turillazzi S, Palagi E. Dominance Interactions in Young Adult Paper Wasp (Polistes dominulus) Foundresses: A Playlike Behavior? Journal of comparative psychology (Washington, DC : 1983). 2006;120:394-400.

13. Jereb P, Roper C, Norman M, Finn J. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids. FAO species catalogue for fishery purposes. 2014;4(3):370.

14. Young JZ. THE NUMBER AND SIZES OF NERVE CELLS IN OCTOPUS. Proceedings of the Zoological Society of London. 1963;140(2):229-54.

15. Young JZ. The anatomy of the nervous system of Octopus vulgaris. Oxford: Clarendon Press; 1971.

16. Rowell CHF. Excitatory and Inhibitory Pathways in the Arm of Octopus. The Journal of Experimental Biology. 1963;40:257-70.

17. Sumbre G, Gutfreund Y, Fiorito G, Flash T, Hochner B. Control of Octopus Arm Extension by a Peripheral Motor Program. Science. 2001;293(5536):1845-8.

18. Packard A, Hochberg FG, Nixon M, Messenger JB, editors. Skin patterning in Octopus and other genera1977.

19. O'Brien CE, Roumbedakis K, Winkelmann IE. The Current State of Cephalopod Science and Perspectives on the Most Critical Challenges Ahead From Three Early-Career Researchers. Front Physiol. 2018;9:700.

20. Di Cosmo A, Pinelli C, Scandurra A, Aria M, D'Aniello B. Research Trends in Octopus Biological Studies. Animals (Basel). 2021;11(6).

21. Cianchetti M, Follador M, Mazzolai B, Dario P, Laschi C, editors. Design and development of a soft robotic octopus arm exploiting embodied intelligence. 2012 IEEE International Conference on Robotics and Automation; 2012 14-18 May 2012.

22. Laschi C, Cianchetti M, Mazzolai B, Margheri L, Follador M, Dario P. Soft Robot Arm Inspired by the Octopus. Advanced Robotics. 2012;26(7):709-27.

23. Maldonado E, Rangel-Huerta E, González-Gómez R, Fajardo-Alvarado G, Morillo-Velarde PS. Octopus insularis as a new marine model for evolutionary developmental biology. Biology Open. 2019;8(11):bio046086.

24. Weidig G, Bush B, Jimenez F, Pelled G, Bush TR. 3D octopus kinematics of complex postures: Translation to long, thin, soft devices and their potential for clinical use. PLoS One. 2024;19(5):e0303608.

25. Richie J, Letner JG, Mclane-Svoboda A, Huan Y, Ghaffari DH, Valle ED, et al. Fabrication and Validation of Sub-Cellular Carbon Fiber Electrodes. IEEE Trans Neural Syst Rehabil Eng. 2024;32:739-49.

26. VanBuren T, Cywiak C, Telgkamp P, Mallett CL, Pelled G. Establishing an Octopus Ecosystem for Biomedical and Bioengineering Research. JoVE. 2021(175):e62705.

27. Kuba MJ, Byrne RA, Meisel DV, Mather JA. When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in Octopus vulgaris. J Comp Psychol. 2006;120(3):184-90.

28. Mather JA, Anderson RC. Exploration, play and habituation in octopuses (Octopus dofleini). Journal of Comparative Psychology. 1999;113(3):333-8.

29. Wood JB, Wood D. Enrichment for an advanced invertebrate. The shape of Enrichment. 1999;8(3):1-5.

30. Zylinski S. Fun and play in invertebrates. Curr Biol. 2015;25(1):R10-2.

31. Wood JB, Anderson RC. Interspecific Evaluation of Octopus Escape Behavior. Journal of Applied Animal Welfare Science. 2004;7(2):95-106.

32. Hanlon RT, Forsythe JW. Advances in the laboratory culture of octopuses for biomedical research. Lab Anim Sci. 1985;35(1):33-40.

33. Forsythe JW, Hanlon RT. Behavior, Body Patterning and Reproductive-Biology of Octopus-Bimaculoides from California. Malacologia. 1988;29(1):41-55.

34. Albertin CB, Simakov O, Mitros T, Wang ZY, Pungor JR, Edsinger-Gonzales E, et al. The octopus genome and the evolution of cephalopod neural and morphological novelties. Nature. 2015;524(7564):220-4.

35. Nowak RM. Walker's Mammals of the World: Johns Hopkins University Press; 1999.

36. Poole T. Happy animals make good science. Lab Anim. 1997;31(2):116-24.

37. Prescott MJ, Lidster K. Improving quality of science through better animal welfare: the NC3Rs strategy. Lab Anim (NY). 2017;46(4):152-6.

38. Moltschaniwskyj NA, Hall K, Lipinski MR, Marian JEAR, Nishiguchi M, Sakai M, et al. Ethical and welfare considerations when using cephalopods as experimental animals. 2007;17(2):455-76.

39. Mather JA, Anderson RC. Ethics and invertebrates: a cephalopod perspective. Diseases of aquatic organisms. 2007;75(2):119-29.

40. Sykes A, Gestal C. Welfare and Diseases Under Culture Conditions. 2014. p. 97-112.

41. Bennett H, Toll RB. Intramantle inking: a stress behavior in Octopus bimaculoides (Mollusca: Cephalopoda). J Am Assoc Lab Anim Sci. 2011;50(6):943-5.

42. Chancellor S, Grasse B, Sakmar T, Scheel D, Brown JS, Santymire RM. Exploring the Effect of Age on the Reproductive and Stress Physiology of Octopus bimaculoides Using Dermal Hormones. Animals (Basel). 2023;13(19).

43. Reimschuessel R, Stoskopf MK. Octopus automutilation syndrome. J Invertebr Pathol. 1990;55(3):394-400.

44. Vidal EAG, Villanueva R, Andrade JP, Gleadall IG, Iglesias J, Koueta N, et al. Chapter One - Cephalopod Culture: Current Status of Main Biological Models and Research Priorities. Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries. 67: Academic Press; 2014. p. 1-98.

45. Ahloy-Dallaire J, Espinosa J, Mason G. Play and optimal welfare: Does play indicate the presence of positive affective states? Behavioural Processes. 2018;156:3-15.

46. Mendl M, Paul ES. Animal affect and decision-making. Neuroscience & Biobehavioral Reviews. 2020;112:144-63.

47. Holst MM, Miller-Morgan T. The Use of a Species-Specific Health and Welfare Assessment Tool for the Giant Pacific Octopus,. J Appl Anim Welf Sci. 2021;24(3):272-91.

48. Mather J, Anderson RC. Personalities of octopuses (Octopus rubescens). Journal of Comparative Psychology. 1993;107:336-40.

49. Burghardt GM. Defining and recognizing play. The Oxford handbook of the development of play. Oxford library of psychology. New York, NY, US: Oxford University Press; 2011. p. 9-18.

50. Bidel F, Bennett NC, Wardill TJ. Octopus bimaculoides' arm recruitment and use during visually evoked prey capture. 2022;32(21):4727-33.e3.

51. Rushen J, Mason G. A decade-or-more's progress in understanding stereotypic behaviour. CABI. 2006:1–18.

52. Burghardt G. On the origins of play. 1984:5-41.

a
b
c
d
e