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Anecdotal Accounts of Manatee Behavior: Conservation and Management, Behavioral Ecology, and Cognition

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Abstract

Herein, we report anecdotes of manatee (family Trichechidae) behavior based upon accounts made by experienced observers. We have categorized the anecdotes into the broad categories of Conservation and Management (interactions with boats, people, and capture nets; rehabilitation and release), Behavioral Ecology (navigation, mother–calf interactions, interactions with conspecifics, mating behavior and birthing, anti-predator behavior, foraging and eating), and Cognition (sensory perception; learning, memory, and knowledge; interactions with objects, other species, and people; and mimetic behavior). These are all subjects that pertain to the goals of the Florida Manatee Recovery Plan of 2001. We found that many accounts report similar behaviors, suggesting that these may be fruitful lines of further inquiry. One subcategory, Navigation, appears to offer many research areas amenable to systematic study. The apparent behavioral flexibility and knowledge shown in manatee actions in several domains suggest that investigations of manatee intelligence are likely to be revealing.

Key Words: manatee, Trichechidae, behavior, conservation, behavioral ecology, cognition

Introduction

I (GBB) still remember the excitement as a child of reading the anecdotes of Raymond Ditmars, Curator of Reptiles at the Bronx Zoo, about capturing snakes. Later, the films of Jacques Cousteau provided an inspiring glimpse of another world under the sea, and Konrad Lorenz's (1967) insights on aggression captured in a snorkeling excursion observing the behavior of reef fish in the Florida Keys alerted me to the possibilities of studying animal behavior. The popular works of John Lilly (1975) and conversations with my tennis instructor (and incidentally a linguist and collaborator of Lilly), Hank Truby, guided me in the direction of marine mammal research.

Later, when I began to study dolphin and whale behavior with Lou Herman, among my favorite readings were the anecdotal ones about the earliest days of cetacean research. These included McBride's fascinating observations of dolphin behavior, particularly their avoidance of nets, which suggested sonic abilities, later called echolocation (reported by Schevill & McBride, 1955).

The anecdotal method does not establish the veracity of observer narratives. Although McBride's suppositions have been confirmed through extensive study of dolphin echolocation, Lorenz's theories on aggression and Lilly's assertions about dolphin intelligence were challenged and substantially refuted. What anecdotes do provide are suggestions for new ways of thinking about animal behavior, and new lines of study and support or contraindication for existing research (Burghardt, 1985). Incidentally, they can provide the inspiration for many young researchers to study animals. As pointed out by Wynne (2004), scientific rigor demands that one stay vigilant of the dangers of anthropomorphizing observations of animal behavior and inferring mental processes. Thus, suggested explanations of manatee behavior (e.g., in terms of "comfort" or "kissing") should be viewed as hypotheses subject to further testing.

Our initial goal in gathering anecdotal accounts about manatee (*Trichechus* spp.) behavior was to provide a basis for generating testable hypotheses regarding manatee cognition (Bauer & Reep, 2022), but the participant responses included in the Supplemental Table (available on the *Aquatic Mammals* website) extend to additional topics, including conservation, management, and behavioral ecology. In this article, we present a variety of anecdotes from experienced observers that help to reveal the extent of individual variation and, thus, the range of manatee behavior. The focus on

specific observations instead of general accounts contributes to a sharper appreciation of this range of individual variability. Rather than attempting to be comprehensive, we aimed to report interesting anecdotes from this admittedly haphazard sampling. The text first highlights anecdotes of primary interest that are relevant to conservation and management, including interactions with boats, interactions with people, behavior around capture nets, and rehabilitation and release. Effective management and conservation efforts rely on grounding in behavioral ecology and cognition. The first of these categories includes navigation, interactions among mothers and calves, interactions with conspecifics, mating, foraging, and defensive behaviors. The second category includes sensory systems, learning, memory, and decision making related to foraging and navigation. The importance of these subjects was recognized by the Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service [FWS], 2001). Many of the anecdotes reported herein are examples that add to existing published accounts (Hartman, 1979; Reynolds, 1981; Marsh et al., 2011; Reep & Bonde, 2021; Marsh, 2022). Many provide hitherto unpublished examples of behavior suggesting new lines of inquiry.

Methods

Participants

We identified experienced observers of manatee behavior through the published literature and personal contacts. Participants were recruited by e-mail, through the international newsletter *Sirenews*, and by word of mouth to participate in an online survey. We also conducted Zoom interviews with some participants, usually in pairs, focusing on the same topics as in the survey. Twenty-six participants were interviewed and/or completed the surveys—16 completed the survey alone, eight participated in interviews only, and two did both. Two other responses came by e-mail to specific questions of ours on release experience, navigation, and auditory behavior. In addition, we both contributed a few anecdotes to bring the total participants to 30.

Procedures

Survey participants answered our questions using the online platform Qualtrics. They were asked to provide demographic information, the nature of their experience (e.g., researcher, field biologist, boat captain), and observations of interesting behaviors that might reflect mental abilities of manatees. We suggested behavior categories for respondents, with the option of discussing other behaviors if our examples were insufficient. The list of categories was based on Bullock's (1986) candidates for cognitive research: *Interacting with the Environment* (manipulating objects, exploration, play), *Social Interactions* (copying behavior, social learning, sharing, aggressiveness, courtship, cooperation, teaching), *Communication* (vocalizations, physical gestures), *Sensation and Perception* (detecting other animals or boats, individual recognition, navigating), *Higher Level Cognition* (planning, emotional behavior, deception, humor), *Problem Solving* (evading nets or avoiding boats), and *Knowledge* (memory for freshwater sites, boat motors, people). The *Sensation and Perception* category was not explicitly indicated by Bullock but did correspond with a major research agenda in laboratory investigations.

Although the Zoom interviews of roughly 1 h were not strictly structured, we frequently used Bullock's (1986) categories as prompts. These interviews were summarized and added to the survey data and e-mail sources to generate 189 brief anecdotes. In this report, "observations" refer to these anecdotal accounts.

We integrated the participant observations with the published literature on behavior. Because much of this literature has been recently reviewed (Marsh et al., 2011; Reep & Bonde, 2021; Marsh, 2022), we frequently use secondary sources to avoid unnecessary redundancy.

Results

We partitioned participants' longer narratives into brief anecdotes in the Supplemental Table. Many of these anecdotes are discussed in the text, cited with a number corresponding to the table. Some anecdotes are not discussed but are listed in the table. Based upon the responses we received, we reorganized the anecdotes into the following categories:

Conservation and Management

- Interactions with Boats
- Interactions with People
- Behavior Around Capture Nets
- Rehabilitation and Release

Behavioral Ecology

- Navigation
- Mother–Calf Interactions
- Interactions with Conspecifics

- Mating Behavior and Birthing
- Anti-Predator Behavior
- Foraging and Eating

Cognition

- Sensory Perception
- Learning, Memory, and Knowledge
- Interactions with Objects, Other Species, and People
- Mimetic Behavior and Social Learning

Species were reported by observers or were inferred from the reported location of the observer. The vast majority of anecdotes were of Florida manatees (*Trichechus manatus latirostris*), although there were some reports of the conspecific Antillean manatees (*Trichechus manatus manatus*) and of West African manatees (*Trichechus senegalensis*). Unfortunately, we did not receive any observations of Amazonian manatees (*Trichechus inunguis*). Unless otherwise stated, we will use "manatee" to refer to the West Indian manatee (this includes Florida and Antillean manatees).

Conservation and Management

Interactions with Boats (1-21)—Boat interactions account for a significant percentage of annual mortality for Florida manatees (see Reep & Bonde, 2021), and manatees across species employ a variety of strategies to avoid boats. For example, they may adjust the time of day when they feed. In Biscayne Bay, Florida, a heavily trafficked area in daytime, they feed at night (1). Antillean manatees in Belize and Cuba use overhanging mangroves to hide when pursued for health assessments (2). Not all manatee–boat interactions are related to avoidance. For example, at Blue Spring, Florida, some manatees have a tendency to "explore" the Florida Fish and Wildlife Conservation Commission (FWC) rescue boat when it enters the spring run instead of swimming away from it, especially when the boat stays still (prior to rescue/capture) (3). This "exploration" might also be construed as vigilance in the presence of a potential threat.

Manatees are responsive to boat noise (Nowacek et al., 2004; Miksis-Olds et al., 2007; Rycyk et al., 2018). In the Hobe Sound area north of Riviera, Florida, manatees swimming in the Intracoastal Waterway time their dives and surfacings to boat passings (4). In the Fort Myers, Florida, area, VHF tracking allowed an observer to monitor manatees as they approached motorized craft and then turned away (5). Over the years, many experienced observers have reported that manatees can recognize individual boats, probably by the sound characteristics of their motors. African manatees in Cameroon quickly avoid navigating boats; hence, boat collisions are uncommon (6) in contrast to Florida manatees that might be encountering a higher density of vessels. There is some variation among reports on the manatee response—for example, maintaining behavior or fleeing—but these variations may reflect differences in boat motor noise spectra, individual behavioral responses, or acoustic environment. In addition, in contrast to reports that manatees move to deeper water in response to threats (Nowacek et al., 2004; Miksis-Olds et al., 2007), a more recent study found that movements toward deeper or shallower water were equally likely (Rycyk et al., 2018). One anecdote reports that manatees appear to adjust the location of their activities by staying close to the banks of waterways (7). African manatees in Gabon and Cameroon flee approaching motorized boats (8) when engine noise increases (9) or when boats are traveling at high speed (10).

Nonmotorized watercraft are also avoided at times. In Ndogo Lagoon, Gabon, African manatees have been observed to flee when they sense the presence of a nonmotorized boat (12). Although African manatees are extremely shy and wary of humans, in several places where hunting has stopped or is minimal, such as in Gabon, Cote D'Ivoire, and Angola, manatees exhibit curiosity about boats and will approach and sometimes hang around a boat (13).

Wayne Hartley reports that, without apparent visual contact, when kayaks are approaching, manatees move out of the immediate area, as if doing a circular dance coordinated with the movements of the kayak, but they still remain in the general vicinity (7). Once, he was filming manatees in Blue Spring, Florida, and wanted to get his kayak around to the manatees' other side, but they kept moving to keep him on the same side (14). Manatees not familiar with Blue Spring (often immigrants from the Atlantic coast) tend to be wary at first of the research canoe (15).

Manatees will also flip kayaks and attempt to flip canoes (16, 17). Hartley reported a manatee at Blue Spring that would reach up above the gunwale to poke him with its flipper, perhaps attempting to flip the canoe (18). There was one manatee in Crystal River, Florida, who specifically attacked red kayaks (19). The substantial variability of manatee behavior around boats, motorized and nonmotorized, suggests a need for systematic investigations to determine the variables affecting their responses to vessels.

Interactions with People (22-38)—Responses of manatees to the presence of people at Three Sisters Springs, Florida, include indifference, avoidance, and curiosity (Syverson & Wolfe, 2016). Syverson & Wolfe (2016) also found that manatees interacted more with each other when humans were absent from the water. These findings have implications for management because human-induced changes in manatee behavior may be stressful, particularly in periods of cold weather when metabolic resources are challenged. There is reason to believe that not all interactions with people are aversive, however.

Manatee tour boat operators in Crystal River often tell their clients that a boisterous crowd of several people is likely to elicit a very different response from a manatee compared to a single calm snorkeler, illustrating that the context of interactions is important. In addition to context effects, many of our observers note that individual manatees exhibit varying degrees of interest in people, some showing strong and play-like attractions. For example, "Georgia" (a Blue Spring manatee) would do things like boost a person up the ladder at the swimming area, grab a pair of jeans off the dock and swim off, and cavort with humans in the water (22). There were several accounts of manatees approaching, nuzzling, goosing, or grabbing people for brief periods (24, 25, 26). In another example (23), Jeffrey Foote, a *National Geographic* photographer, had a manatee, "Floyd," become attached to him, and it followed him everywhere.

Tom O'Shea recalls that "Howie," a manatee who had flipped him out of a canoe, was a very curious adult male notorious for clasping every snorkeler he came across and attempting to clasp other manatees as well (26). He would often get in the way as O'Shea swam trying to get ID photos or body length measurements of other manatees. Bengtson and crew nicknamed him "Horny Howie" in the ~1979-1980 period. They attributed Howie's "curiosity" in part to a mating drive. He was often a participant in cavorting (mating) groups. Howie's tolerance and interest in people also seemed to be a "lifelong" trait (26, 27). As is now increasingly recognized for other species of mammals and birds (O'Shea et al., 2022), lifelong behavioral characteristics support the concept of stable individual "personalities" (behavior patterns) in manatees.

Manatees sometimes lift people out of the water (22, 23, 28, 29). Jeffrey Foote was standing in the water attempting to photograph other manatees when Floyd swam up behind him and through his legs, lifting him up (23). In Blue Spring, Florida, Monica Ross was trying to free tag a female when another female swam underneath her, lifting her out of the water. Then, six other females lined up facing Ross as if watching her and the interactions. This could be an example of vigilance behavior. Many males were also in the spring but did not engage (28).

In contrast to the boisterous interactions sometimes described, manatee–human interactions may also be of a calmer nature. I (RLR) was in the water with a tour group at Kings Bay, Florida, and there were many manatees in the vicinity. I was near one that was lying upside down at the surface. It took my hand gently in its flippers and placed it on its chest—very peaceful and calm (Reep, pers. obs.). Tom O'Shea reports the ease with which Bob Bonde and he retagged the same manatee 33 times over nearly 8 y (27), another example of pacific interactions with people.

Eye contact might represent another type of interaction between manatees and people, although this behavior appears to contrast with what we know about their visual acuity (Bauer & Reep, 2022). For example, some of our participants report that some manatees respond to eye contact (30-33). Descriptions variously described visual monitoring and tracking or avoidance of human staring.

Reports indicate that African manatees in the Senegal River also approach people at the edge of the river, including women washing clothes or dishes, and children who are swimming (34).

Behavior Around Capture Nets (39-47)—Nets are used to capture manatees for health assessments, radio tagging, and to bring injured manatees into a rehabilitation facility. Manatees may evade capture nets by swimming around or under them (39, 40). In some cases, they swim directly through the net, creating a hole (40), a behavior that has also been observed in Belize (40) and Africa (41, 42). In Lake Ossa in Cameroon, manatees will move along a fishing net trying to find a way around it to go to the grazing site. If the net is long, they will break through it (42). At Blue Spring, Wayne Hartley has observed manatees waiting in shallow water until capture-netting is done so that they can get access to the spring (40). In Port Everglades, Florida, manatees will often move toward shallow water when capture nets are present (40). Some manatees will retreat into the herd to avoid capture (40), a common anti-predator strategy in other species (Wilson, 1975).

Escape from nets is frequently reported. Monica Ross observed a set of responses to nets by a manatee that reflect learning. The first time it was captured, the manatee got knotted up in the net. The second time, it worked the lead line. By the third time, it was completely savvy, going over and under the net (43). Manatees will dig their noses into sand and go under as well as lie

sideways so that the net will go right over them. They also learn the capture routine: they follow the boat and then move toward the net opening. In a possible example of mimicry, one animal got out of the net and an observing animal followed by the same route (43). This type of learning sequence may eventually lead to manatees avoiding capture in the first place. Some manatees are amenable to multiple captures, whereas others become evasive (44). O'Shea reports that manatees at Blue Spring became very "edgy" for days after capture events. A few days after one capture, a different disturbance in the water caused a manatee stampede, with those present swimming rapidly down and out of the spring run and "screaming" into the hydrophone as they passed by, possibly communicating fear and warning to others (45).

Rehabilitation and Release (48-54)—Manatees that have undergone rehabilitation for boat injuries, emaciation, or cold stress often exhibit behavior that is different from that of normal wild manatees (see Reep & Bonde, 2021). For example, manatees released from rehabilitation will watch cavorting or mating herds but not participate themselves (48). Released calves will follow other manatees around until they get the hang of the navigation routes (49). Released juveniles will stay with a mother–calf pair for 7 to 10 d, but they will not try to nurse (48).

A cold-stressed female was rescued and tagged upon release at Blue Spring, Florida. She had a calf the summer after her release. When she returned to Blue Spring the following year, she tried to park her calf (leave it in a specific area in order to forage alone or otherwise seek solitude) four times, but it kept following her. The fifth time she parked it, left, and then turned around and stared at the calf. It remained behind as if obeying (50).

"Stormy" was born in and lived in captivity for 17 y. On first release into the wild, he never left the spring where released. He was recaptured and, on second release, he joined up with "Georgia" and her calf at Blue Spring. When Georgia and the calf swam from the clear spring water to the dark water of the river, Stormy stopped and would not follow. He approached a second time and balked again. He "burst" through on the third try and caught up to Georgia and her calf. There was only a small difference in temperature between the clear and dark water, ~0.5ºC (51).

In Puerto Rico, "Moises" was raised in captivity and then released into a sea pen. He was given a yellow and blue boogie board for enrichment, which he used for masturbation. After he was released into the wild, he became similarly enamored of yellow and blue boogie boards, kayaks, other boats, and jet skis (52).

During release, after almost 3 y in rehabilitation for a watercraft injury, "Lesley" would roll herself onto her back to prevent the veterinarian or release staff from touching the area of the healing wound. She traveled in the truck to the release site on her back and was released on her back at Blue Spring (53).

"Two Notch" swam upriver to Manatee Springs State Park and stayed for 6 wks. This individual seemed to enjoy being around Susan Butler, so Jim Reid was able to free tag it. After that, they had difficulty getting close to him again (54).

Some behavior transfer between captive and natural environments, such as eating natural foods, is desirable. Other behaviors, such as attraction to humans in captivity, can be injurious or unhealthy in the wild—for example, if manatees approach boats or are attracted to people providing nonnutritious foods. The animal learning literature is clear about certain types of transfer: habituation and extinction do not transfer well. In fact, the switch to a new environment will probably cause dishabituation and recovery of extinguished behavior (see review in Bauer, 2005). In contrast, aversive learning does transfer well, so we might expect blood draws and physical restraint to promote some aversion to humans. The case of Lesley maintaining a protective inverted posture even in the release truck (53) suggests such transfer. It would be informative to see how she responded to people after release to observe how her captive experience influenced her behavior. The outcome from transfer of positively reinforced behaviors among animals is mixed. The case of Moises continuing to be attracted to yellow and blue boats is an example of undesirable transfer of a positive experience. However, the similarity of a sea pen to natural conditions suggests that the main obstacle for transfer, difference in environments, was minimized. Fellner et al. (2006) found no transfer of behaviors trained in a captive habitat to the wild. Since capture and release of manatees is such a frequent occurrence, careful investigation of behavioral transfer is an important area for future research. A better understanding of the sensory processes related to avoidance and escape from nets might reduce the stress of capture for rehabilitation purposes.

Behavioral Ecology

Navigation (55-65)—Successful navigation by manatees is necessary for finding food resources and warmwater sites, activities that are fundamental to surviving and thriving. Tracking studies have been essential for developing effective conservation and management of critical manatee habitat (see Marsh et al., 2011; Reep & Bonde, 2021). Anecdotal accounts suggest that manatees are very purposeful in their navigation. Data from tracking studies and resightings of known

individuals indicate that manatees find their way to specific sites that are used for feeding, rest, sanctuary (no humans present), and thermal refuge (Weigle et al., 2001; Deutsch et al., 2003; see also Marsh et al., 2011; Reep & Bonde, 2021).

Dead reckoning is straight-line travel between two locations. In the absence of obvious environmental cues, its occurrence suggests intriguing hypotheses. In one instance, a manatee in Belize was observed moving in a straight-line fashion over deep ocean water for 27.4 km to reach a particular location, then turned around and used the same trajectory to return to the starting point. This occurred at night (55). Other manatees in Belize would travel directly to a specific river (56). Similarly, two manatees on the Gulf Coast of Florida were observed traveling in a straight line across open water for ~160 km to reach the mouth of the Suwannee River rather than following the longer contours of the shoreline (57). "Washburn" was found off the north side of Cape Cod. He was relocated to the central Atlantic coast where there were other manatees. He stayed there awhile and then went out Ponce Inlet and down to Cape Canaveral. He went out farther east and took a straight-line trajectory to the Bahamas. This included night travel (58).

Contrasting travel characteristics are presented by Florida manatees in the St. Johns River, Florida, that have been observed moving parallel to the shore, bypassing several creek inlets before turning to enter a specific creek, indicating preference for and knowledge of a particular location (60, 61). Similar travel is seen in the habitual patterns of manatee navigation in connection with feeding. Manatees in Kings Bay were often observed traveling ~19 km out to estuarine grass beds in the late afternoon and then returning to the bay by morning (62). In the Ten Thousand Islands region on the Gulf Coast of Florida, GPS tagging studies have shown that individual manatees utilize a few different paths between inland freshwater sites and preferred seagrass beds, and these paths often vary across individuals (Reid et al., 2003; Stith et al., 2006). Rycyk's observations (64) that manatees trace the borders of canal systems and, in one case, found a narrow break in seagrass to traverse suggest possible tactile or hydrodynamic guidance, although vision might be of use in daytime and in clear water. Careful mapping of manatee routes onto topographic maps of underwater terrain in conjunction with visibility assessments might elucidate the role of hydrodynamic reception.

At a longer temporal scale, manatees engage in seasonal movements to find reliable thermal refuges during the cooler months. A calf learns these seasonal movements during its ~2-y period of dependency when it follows the movements of its mother. Tracking and resighting studies have shown that individuals exhibit site fidelity: they engage in the same pattern of movements to the same sites over many years (Weigle et al., 2001; Deutsch et al., 2003), an indication of spatial knowledge.

The long-distance travels of the manatees "Chessie" (Reid, 1995) and Washburn (Deutsch et al., 2022) from Florida to the northeast coast and a few other similar cases define the known maximum extent of manatee navigation. Chessie revisited some of the same sites on subsequent travels over several years, so it appears that to some extent his movements were site-directed rather than being random wanderings (Reid, 1995; Deutsch et al., 2003; Reep & Bonde, 2021).

Movement patterns of manatees have been investigated extensively and have revealed an ability to navigate complex environments and to travel long distances, sometimes traversing areas that are relatively featureless to humans. There are important conservation implications to understanding naturally occurring manatee travel. For example, to what extent do manatees travel to seek other sources of food when a preferred food source is unavailable (e.g., due to overgrazing, storm disruption, or algal overgrowth)? Currently, this is an important issue for manatees in the Indian River Lagoon. A sharp decline in water quality has promoted algal growth and has thus diminished the viability of submerged aquatic vegetation upon which manatees feed. Consequently, 2021 saw a dramatic increase in the number of emaciated manatees and manatee deaths due to starvation in this region (FWC, 2022; Mazzei, 2022).

Observations of manatee movement patterns indicate a degree of flexibility in choosing successful paths as well as individual variation. It may be that manatees use landmarks in these nearshore environments like contours of the substrate and water current patterns, acoustic beacons, salinity gradients, or other chemical traces to recognize previously used paths. The sensory mechanisms underlying straight-line travel in open water by an animal with limited visual acuity, traveling at night or in deep, murky conditions, remain unknown. Research with other species such as baleen whales suggests that the mechanisms may be complex, including geomagnetic (Walker et al., 1992), oceanographic, and gravitational (Horton et al., 2020) cues.

We also need laboratory studies to determine the mechanisms that might guide manatee orientation. How manatees might use specific senses to determine motor behavior can be investigated using a variety of standard techniques such as t- and starburst mazes, as well as variations of the Morris water maze. For example, tactually or

hydrodynamically detectable objects can be presented in a maze while controlling for other senses to determine directional movement. Although maze tasks can be implemented in many oceanarium settings, a large enclosed lagoon or spring, such as Homosassa Springs, Florida, might more easily accommodate these experiments with large animals such as manatees.

Psychophysical testing of magnetic detection by pigeons and other species, which is largely based on instrumental conditioning, has proven difficult in the laboratory, despite the fact that manipulations in natural settings have supported magnetic sensitivity (Wiltschko & Wiltschko, 1995). Therefore, a more fruitful approach for initiating investigation into the sensory processes involved in straight-line travel might involve correlational investigations of natural travel—for example, mapping migrations over geomagnetic topography such as has been done with humpback whales (Horton et al., 2020). Spatial navigation also provides an opportunity to investigate gerontological cognitive dysfunction in manatees. Decline of spatial memory with age in humans and other animals (Barrash, 1994; Hopkins et al., 2021) is a common finding. This characteristic is also paralleled by loss of hippocampal volume and cholinergic efficacy. The behavioral aspects of this decline can be studied by working memory tasks such as maze navigation, while the neurobiological impact can be studied with brain measurements (see Cook et al., 2015, for an example of an integrated behavioral and neurobiological approach). These studies, in turn, would have implications for manatee navigation across the life-span.

Mother–Calf Interactions (66-81)—We received many anecdotal accounts of mother–calf interactions. Mothers, who typically have only one calf at a time (Marsh et al., 2011), are often observed to park their calves. In Port Everglades, Florida, it was common to see several calves parked in the basin with mothers out feeding before they would come back to where the calves were located (66). In one case, five or six calves were parked at Blue Spring, Florida. All the calves would go out to meet a mother when she returned (67). In a cautionary tale, an "orphaned calf" in the Dominican Republic was picked up and brought to the national aquarium. Later, a large manatee was seen hanging around the rescue location. Aquarium staff took the calf back, and the next morning they saw the calf with the large manatee, likely its mother. So, parking can be confused with orphaning (69).

When alligators are present, a mother will position herself between the alligator and her calf (T. O'Shea pers. comm., as referenced in Marsh et al., 2011) (70). In one instance, Pat Rose observed a 3.6-m alligator positioned over a calf. A large female got underneath the alligator and lifted it out of the water. There was no change by the alligator, so she did it again—also with no change. Finally, the female lifted the alligator again, higher. The alligator moved away, and the female followed it (71).

Mothers exhibit nurturing behavior toward deceased calves. In Florida, they have been observed pushing deceased calves through the water (77) and lingering near a calf carcass while exhibiting subdued behavior (78). One mother came to Blue Spring for about 10 d after her calf's carcass had been removed (78).

Interactions with Conspecifics (82-96)—Several observers reported examples of "kissing" behavior in greeting (82), suggesting tactile or perhaps chemical communication. Manatees in the St. Johns River were observed to come from separate locations and meet nose to nose. They used a direct approach in low visibility and did not circle; localization was precise. They were in the middle of the river so were not following shallow water physical cues (83), which suggests they were using auditory or chemical ones. From a boat in St. Mary's, Georgia, Tiare Fridrich often saw manatees that were actively swimming until they met up with another manatee, at which point it appeared they would investigate each other. If that manatee was not the one the other was looking for, it would continue to swim until it found a specific animal (84).

Manatees sometimes appear to provide aid and comfort to conspecifics (85); this is often called epimeletic behavior. In one case, an injured medium-sized adult manatee was observed near a bank in Magnolia Springs, Crystal River, Florida. Two other similar-sized manatees "bracketed" their injured comrade and provided support and protection (86). In one instance, a female that had lost her calf appeared to be comforted by a juvenile manatee for several days (87). Wayne Hartley also reports examples of comforting behavior (88).

Other examples of interactions are more difficult to interpret. Kerry Sanchez reports that five to six males were observed interacting with a deceased manatee, but the behavior did not appear to be comforting (89). In another example, Pat Rose and Cora Berchem observed males in mating and cavorting herds attempting to mate with deceased females of varying degrees of decomposition—from fresh to moderately decomposed (2018, 2019, and 2020 during the late spring and summer months; reported by the public via a stranding hotline). The animals had been observed for several days in some instances (in 2020) and in groups ranging from two males to a minimum of five males. These examples were confirmed via video sent by the public and via in-field observations by responders (90).

Play-like behavior among manatee conspecifics includes taking turns interacting with objects such as crab trap buoys, plastic bags, anchor lines, and sticks (91, 92). In one case, two manatees in Blue Spring, Florida, found some pantyhose and were playing with it while keeping a third manatee from getting it as if playing keep-away (93).

In other instances, Mike Birns observed manatees cooperating to move a piece of driftwood blocking the egress at Three Sisters Springs (94), and two tagged male manatees would always be seen together as if they were buddies (95). Apparent active searches for specific individuals, epimeletic behavior, and a report of male "buddies" are inconsistent with the generally held assumption that adult manatee group stability is low (see Reep & Bonde, 2021). This may be a fruitful line for further investigation of individual differences in affiliative behaviors.

Mating Behavior and Birthing (97-101)—Male manatees have been observed rubbing their genital area on people, kayaks, pontoons, pilings, and dead manatees, sometimes while exhibiting penile erections (90, 98-100). Female manatees in estrous frequently try to avoid males, and pregnant females often choose quiet locations for giving birth (Hartman, 1979; O'Shea & Hartley, 1995; Rathbun et al., 1995; Reid et al., 1995). It is suspected that females about to give birth may hide to avoid roving males that might benefit by the death of the newborn (O'Shea & Hartley, 1995). Don Dematteis describes a female with a very young calf, under 1 mo old, being harassed by an aggressive male. He had already forced her to beach in shallow water to protect the calf. He then drove them into a small side canal (16). In another instance, a female manatee beached in a New Smyrna, Florida, inlet to avoid a mating herd; the males waited in the water for her to return (101).

Anti-Predator Behavior—Manatees suffer predation in parts of their range from sharks, crocodilians, jaguars, and humans (Marsh et al., 2011). Reports of non-human animal predation on Florida manatees are rare, but they probably retain the defense mechanisms from earlier evolutionary times of more frequent danger. No formal studies of predation on manatees have been done to our knowledge. Marsh et al. (2011) discuss the physical characteristics (e.g., size, thick skin) that protect manatees, behavioral strategies (fleeing from danger), and anecdotal reports of interactions with predators. The anecdotes we have collected complement, supplement, and, in some cases, contrast with previous reports, providing a glimpse of the protective strategies employed by manatees, including defensive behaviors (avoidance and escape), aggression, and possible cases of exploration, inspection, and wariness that might inform manatees about future encounters with potential threats:

- *Defensive Behavior: Avoidance* (102-103)—Manatee defensive behavior anecdotes cover responses to other species, including people, and boats (1, 2, 4, 6, 7, 11). Nicola Erdsack watched manatees in Crystal River, Florida, frequently avoiding swimmers and snorkelers, including herself, diving so close under a person that physical contact seemed unavoidable but did not happen. She observed this in both clear and totally murky water—for example, snorkeling back to the U.S. Fish and Wildlife Service (FWS) pontoon pavilion at King Springs, Florida, not seeing a single manatee, she got up on the platform and saw that she had swum through a group of three manatees without noticing (102). Some manatees will avoid or leave if you stare at them. Some will look away and then return to looking at the person (30). In Weeki Wachee, Florida, Jennifer McGee has seen manatees grouped in an area where humans do not usually go to avoid people who come into the area (103).

- *Defensive Behavior: Escape* (104-105)—An unusual example of manatee defensive behavior in response to sharks was reported by Holly Edwards. During a manatee distribution survey, she witnessed two adult manatees and one small calf in St. Joseph's Sound in Clearwater, Florida, being pursued by 40 or 50 small sharks (species unknown). The sharks were swimming quickly when they approached the three manatees; the adult manatees stopped swimming and positioned themselves between the sharks and the calf, with noses toward the calf and tails out as seen in some whale species (e.g., Pitman et al., 2001). The sharks approached at a high rate of speed to within about 6 to 9 m of the manatees and then suddenly retreated (104). We know sharks are a threat based on shark bite scars on Florida manatees (105).

- *Aggression* (106-111)—Aggression in a slow-moving herbivore without cutting teeth or claws is manifested in some interesting ways. Alligators attack manatees rarely or not at all in Florida (106); nevertheless, manatees display caution and at times show seemingly aggressive behavior toward them. As noted earlier, Florida manatee mothers typically place themselves between their calfs and alligators, suggesting protection from a predator (70) (T. O'Shea, pers. comm., as referenced in Marsh et al., 2011). Tom O'Shea has recorded

changes in manatee vocalizations in the presence of alligators (81), perhaps communicating the threat of danger to other manatees.

Our observers reported instances of manatees lifting alligators or harassing alligators, which suggests aggression, although other observations of lifting birds and people (107) are less easily characterized. In Pat Rose's observation of a female lifting a large alligator (71), the female clearly wanted to move the alligator away. In another example, a manatee followed a 2.1- to 2.4-m-long alligator, which got away onto a log. The manatee investigated its tail, and then went belly up and flipper waved in the face of the alligator (108). In another report, an alligator was resting, and several adult manatees were "playing," rolling over the alligator, which left after about 20 min. The next day, juveniles tried to "play" with the alligator, but it left right away this time (109). Although some observers describe the manatee behaviors as play, the alligators do not appear to share the same perception.

Female manatees have swum between Pat Rose's legs and lifted him up. He described it as very deliberate as if the manatees wanted to engage (110). Observers generally treat this as play. Monica Ross contrasts it with head butting of people or boats, which appears to be aggression. See anecdotes 17 through 19 for other examples of aggression toward boats.

We received one report of aggression, possibly initiated by the presence of a human. Two females fought over who got to play with a male in-water guide. They went so far as to nip each other's tails when they felt the other was hogging him all to herself (111).

- *Exploration, Inspection, and Wariness* (112-113)—Some of the behaviors we have described as aggression might also be construed as exploration or inspection—for example, harassing an alligator or poking a person in a canoe. Wariness characterizes manatee behaviors in a number of contexts. Although African manatees are extremely shy and wary of humans (with good reason!), in several places where hunting has stopped or is minimal, they exhibit curiosity about boats and will approach and sometimes hang around a boat (13). In one region of the Senegal River, manatees are not hunted, and people there believe manatees were once human so they respect them. The manatees are curious and not afraid here (34). In Cuba, hunting still occurs in places, so wariness may in part be due to prior experience with humans (2).

  Manatees may observe alligators, but they appear to be prepared for a rapid exit. Pat Rose and Cora Berchem report an instance of manatees watching an alligator hunt. The alligator stayed still until it made a sudden movement to catch a fish. The manatees startled and fled (112). Perhaps observations serve the purpose of learning how predators behave.

  Individual differences and experiences apparently affect wariness and avoidance. Wayne Hartley reports that early Florida manatee researchers said they would shine a light in the Blue Spring boil at night to see how many manatees were there (they avoided it during the day due to human swimmers), and the manatees would scatter, which might reflect retained learning from early human predation. Nevertheless, currently, the manatees in Blue Spring are accustomed to humans and mostly ignore them (113). Jennifer McGee reports that some manatees are alright with multiple captures and health assessments, even though subjected to semi-invasive procedures like blood draws (44). In contrast, Hartley has seen the opposite—manatees captured once and then not frequenting the area for years (44). For example, a manatee, "Lucille," started out very friendly but became distant as more direct interactions occurred (e.g., detangling a flipper) (44). Therefore, we see examples of both habituation and sensitization to people.

  To the extent that anti-predator behaviors may be employed in evasion of motor boats, a primary anthropogenic killer of Florida manatees (FWC, 2021), a formal study of manatee agonistic behaviors would contribute better understanding of responses to boats and better protection of manatees.

Foraging and Eating (114-123)—Many of our anecdotes are consistent with the thorough review of diet by Marsh et al. (2011); a few examples supplement their description. African manatees are reported to eat a variety of non-plant-based items; for example, Lucy Keith-Diagne (as reported by Tom O'Shea and Buddy Powell) reports they will take fish out of fishermen's nets, and they eat clams regularly—in some specific locations, they are up to 40 to 50% of their diet (114). Keith-Diagne also reports that in Senegal, manatees may be getting scraps of food from dishes being cleaned. They also congregate around cows, perhaps for purposes of coprophagia. This region of Senegal is desert/Sahel outside of the river; there are very few aquatic plants, particularly in the

dry season, so manatees may take advantage of any potential food (34). Buddy Powell also saw African manatees attracted to hippos in the water, ingesting their feces (115).

Among West Indian manatees, eating animal life is less common. However, manatees in the Florida Keys eat scraps of fish at places where humans are cleaning them (116). They will also apparently sample unusual foods; for example, Beck reports that one manatee, "D-Cow," ate a rat (117). Manatees also root through the underwater substrate, eating sand or clay as reported for African manatees (118). Tom O'Shea sometimes observed manatees at Blue Spring ingesting manatee feces when confined to the spring during long cold spells (119). We have also observed this behavior frequently among captive manatees (Bauer, pers. obs.).

As Marsh et al. (2011) point out, "West Indian manatees are certainly not fussy eaters!" Sometimes this broad palette may work to the manatee's disadvantage. Wayne Hartley reports two examples of manatees eating and swallowing rope (120). A manatee was seen with 0.6 m of rope hanging out of its mouth. A researcher grabbed and pulled it, resulting in about 1.8 m coming out. Another manatee was seen with 0.3 m of rope hanging out. These two examples of eating and swallowing rope (120) present a threat of gastrointestinal blockage.

The sound of a broken branch often attracts manatees (121). Sound presumably suggests availability of food as when a mangrove branch drops. They are also attracted by the sound of munching on food (121). Their ability to discriminate between the types of food being eaten is suggested by a study done by an undergraduate New College of Florida student, Kirstin Ohlsen (unpub.). She tested seven undergraduate students on auditory discrimination of manatee chewing sounds of six common laboratory foods—apples, beets, carrots, kale, lettuce leaves, and head of lettuce—recorded at Mote Marine Laboratory. The students were able to discriminate among the sounds of apples, beets, lettuce leaves, and heads of lettuce above chance. The ability of students, inexperienced at discriminating manatee chewing sounds, to distinguish among foods, suggests that manatees would be able to do the same, if not considerably better.

Cognition

We addressed manatee cognition in the wild in a recent manuscript (Bauer & Reep, 2022). In this section, we emphasize the anecdotal evidence for manatee cognition in contrast to experimental evidence from laboratory and field studies included in our previous manuscript.

Sensory Perception—Behavioral and neurobiological laboratory evidence indicates that manatees have exquisite senses of touch and excellent hearing. Their visual acuity and sensitivity are modest, although they do have dichromatic color vision, an apparently unique characteristic among marine mammals. Physiological evidence suggests that their chemical senses are unremarkable, while prior naturalistic observations suggest they may provide greater functionality than suggested from laboratory studies. The senses are comprehensively reviewed in several recent publications (Marsh et al., 2011; Bauer & Reep, 2017, 2022; Bauer et al., 2020a; Reep & Bonde, 2021):

- *Touch* (124-126)—Touch works in an active mode in which manatees initiate action, and in a passive mode in which they detect changes in water movement. For example, in the active mode, tactile guidance of the flippers is suggested by an observation of a manatee rolling a t-shirt (93). The passive mode is suggested by several observers who reported that manatees navigate around objects and people without touching them, even in dark water (124). One of us (RLR) reported how an adult manatee moved its lower body and paddle tail laterally to avoid contact with a 0.6-m pole sticking up from the substrate, suggesting tactile guidance of motor action. Other observers note that manatees are hard to approach and may twitch their tails when they sense a person (125), which may facilitate assessment of people-generated water movement. They may also sense people at a distance, approach to investigate them, and then turn away, even in murky water (126), suggesting tactile mediation.

- *Hearing* (127-132)—Manatees are responsive to a variety of ambient sounds—for example, hoses, clickers, and breaking branches (121, 127); this provides some insight into how the sensitive hearing demonstrated in the laboratory functions in the wild. Not surprisingly, they respond to boats (4, 6, 8, 9, 10, 128, 129) as discussed earlier. Anecdotes support hearing abilities that allow discrimination of amplitude (9) and changes in engine noise (10), localization of boats (4), identification of boats (130, 131), and even identification of the sound of trucks used in capture (132). Monica Ross and Nicole Bartlett (128) report that because some manatees can recognize specific boats, field biologists have to switch boats to get near them. Buddy Powell (131) notes that after several days of captures, manatees in Belize will relocate as if recognizing

the boat noise. In contrast, Bob Bonde and Cathy Beck note that manatees recognize individual boats and may maintain ongoing behavior but may leave in response to novel boat sounds (130).

Jennifer McGee (132) reports that two manatees ("Bonnie" and "Dooley") that were chronic entanglers came to recognize the rescue truck's sound and would leave when it showed up at the boat ramp but not when other vehicles were at the ramp. This implies that they recognized individual truck sounds. In another interesting example of hearing of in-air sounds, Lucy Keith-Diagne (34) reports that women in a village in Senegal told her they have a song they sing to call the manatees.

- *Vocalizations* (133-140)—Although not a sensory modality, vocalizations are integrally related to hearing, so the topic is included here. Structurally, manatee vocalization characteristics are similar across manatee species (Rycyk et al., 2021). Their usage is reviewed in recent publications (Marsh et al., 2011; Reep & Bonde, 2021; O'Shea et al., 2022). Many of the anecdotes reported in the Supplemental Table have been noted in the vocalization literature, so they are not reported here.

  Lucy Keith-Diagne reports an orphan African manatee calf that emitted high-pitched squeaks when she entered the water (133). Tom O'Shea (134) also reports that a captive orphan in the Ivory Coast made high-pitched squeaks when people entered the water to bottle-feed it. Recordings of these squeaks seemed similar to those of *T. manatus* calves. Ultrasonic vocalizations have been reported to occur in Antillean manatees (Ramos et al., 2020), and this seems to be a fruitful area for further investigation.

  Kerry Sanchez (135) notes that vocalizations in transport trucks (2012 to present) were observed in approximately 25% of transportations of healthy manatees (i.e., transfers between facilities, to release sites, during relocation). They observed this between same and different sex pairs and pairs of differing age groups. Vocalizing occurred in the majority of cow–calf transports and appeared to increase in frequency when calves were transported in pools of water not touching the cow.

  In an example of a possible different function for vocalization, Mike Birns (136) watched two adolescents interacting. When the younger one started up a canal with unfriendly human residents, the older one squeaked a possible warning signal. The younger one turned around and did not go up that canal. Birns noticed this behavior 3 d in a row in Crystal River.

- *Vision* (141-142)—Laboratory studies of vision indicate a modest visual neural substrate, poor acuity, and brightness sensitivity similar to fur seals (Griebel & Schmid, 1997; see review of vision in Bauer & Reep, 2017). However, their color vision may enhance some performance characteristics (Bauer & Reep, 2022).

  Our experienced observers reported unexpected visual recognition and tracking abilities. For example, maintaining eye contact and tracking eye movements might seem beyond the capabilities of a species with acuity of only 20 arc minutes (about 20/400 Snellen vision) (Mass et al., 1997; Bauer et al., 2003). Nevertheless, Monica Ross (30) reported that manatees spin around and look at her. They look away or leave if a person maintains eye contact. Some will look away and then return to looking at the person. Cathy Beck (33) confirms that manatees maintain eye contact, and Pat Rose (31) reports that manatees visually track (with a still head) people and eye movements. Jim Reid (141) reports an instance of a manatee, Two Notch, who approached from a distance but, at 12.2 m away, turned his head as if looking at them with first one eye then the other, and then turned around and swam away. Another observation of ostensible visual behavior suggests some caution: a manatee put its eye against Ross's mask (30), a near-field behavior of an emmetropic/hyperopic species (Bauer et al., 2003; Murphy et al., unpub. report) that should preclude focused vision. All of these examples suggest a need for a more detailed assessment of discrimination and tracking under controlled conditions, including use of color stimuli.

  It is difficult to separate color vision from other visual cues such as brightness, but two examples suggest use of hue. Moises, the manatee that developed an attraction for yellow and blue colored boats and other water recreation vehicles in Puerto Rico (52), displayed a spectral preference consistent with manatee color vision (Griebel & Schmid, 1996). In another example in Blue Spring, the manatee Howie saw a hyacinth (*Eichhornia crassipes*), a blue-lavender flower with a yellow center, against a black wet suit and swam directly for it from a distance of about 7.6 to 9.1 m (142), perhaps indicating that the blue and yellow colors made it stand out.

  Finally, in an example that was reported earlier, Stormy abruptly stopped following

another manatee at the transition from clear to dark water, suggesting sensitivity to brightness differences (51).

- *Chemical Senses* (143-144)—Underwater, manatees would probably be using taste, while both taste and olfaction would be available in air. Cora Berchem (143) observed manatees rubbing their belly and genital area on things, suggesting the possibility of scent marking. Although the neural substrates for olfaction suggest limited sensitivity by manatees, "Snooty," a captive manatee, was very interested in mint gum (144). He also liked to bury his rostrum in people's hair and showed inhalation behavior that looked much like sniffing (Bauer, pers. obs.). At this time, the chemical senses of manatees have not been well investigated. Psychophysical testing would help us interpret natural behavior.

Learning, Memory, and Knowledge (146-159)—We incorporated a number of anecdotes into a recent cognition paper (Bauer & Reep, 2022). It is worth revisiting these to provide the original source material (see Supplemental Table), to add anecdotes not reported in the cognition manuscript, and to reframe some of the material to allow for different perspectives.

The anecdotes reveal a range of learning, including avoiding and escaping from nets (39-47). Learning how to escape from nets can be relatively easily explained by associative processes, but the sensory processes involved remain obscure. A learning deficit might be suggested by manatees' putative inability to learn about boats, but Pat Rose and Cora Berchem suggest otherwise. They observed that more heavily scarred manatees show greater hesitancy around boats, an indicator of aversive learning, suggesting that boat strikes may have more to do with compromised sensory processing such as hearing in complex sound environments or natural responses to threat. Several anecdotes indicate knowledge of event timing such as feeding time (148), opening of locks and flood control gates (149-151), and movement of tides (152-155).

Teaching is difficult to establish in the wild (Caro & Hauser, 1992). Nevertheless, teaching-like behavior has been observed by manatees. A mother banged the head of her calf when it approached a diver (80). Lucy Keith-Diagne (151), in another example of guidance-type behavior, observed two manatees surface outside a canal water control lock. The lock doors opened for a boat, and one manatee entered. When it saw the other manatee was not following, it turned around and nuzzled its face. The next time the door opened, the first manatee entered again, and the other one followed this time. They then swam to the downstream doors, waited for them to open, and then both swam out.

Memory for various locations, such as warmwater springs and power plants, food sites, and fresh water, are reported in the literature (Marsh et al., 2011; Reep & Bonde, 2021) and supported by many of our anecdotes about African and West Indian manatees (156-158). Navigation also presents many examples of rich spatial memory and knowledge. A curious example of spatial cognition was provided by a training event with captive manatees. The manatees were putatively trained on command to swim through a hoop, which had been located in a single location. When the hoop was moved, the manatees did not swim through the hoop but swam along the path where the hoop used to be (Bauer, pers. obs.). This might just be a training anomaly but also might suggest that spatial cues for orientation need more investigation.

Interactions with objects, conspecifics, other species, and people, including mimetic behavior, suggest more complex areas of cognition (Bauer & Reep, 2022). Some of these anecdotes were presented above in the category "Conservation and Management." Here, we view them from a cognitive perspective.

Interactions with Objects, Other Species, and People (160-184, also see 22-38)—In our recent cognitive paper (Bauer & Reep, 2022), we described a variety of interactions as play. Play is actually a complex activity that requires rigor to identify (see Burghardt, 2005). Although a manatee appears to have demonstrated Burghardt's (2005) basic requirements for play in a captive situation (Bauer et al., 2020b), we have decided to opt for a more cautious approach to descriptions of play-like behavior by simply referring to them as "interactions." We left our participants free to interpret behavior as play, which many of them did; they are experienced observers looking at behavior within a framework of previous observations and within a specific context. Nevertheless, play, an important aspect of cognition and behavioral ecology, is a research area in need of future study. Interactions with conspecifics is reviewed under "Behavioral Ecology"; here, we review interactions with objects, other species, and people:

- *Interactions with Objects* (160-177)—Manatees investigate, explore, and manipulate a variety of objects, including rocks, sticks, logs, palm fronds, grasses, cinder blocks, rope, hydrophone cables, crab trap lines and buoys, boats and boat paraphernalia (anchor lines, fender buoys, paddles, propellers), boat and dock ladders, diver hair, hands

and feet, diver equipment (e.g., flippers, masks, snorkels cameras, wet suits, dive flags), tag belts and floats, and assorted debris (e.g., plastic bags, signs, transect markers, shirts, socks, panty hose) (21, 91, 160-177). The actions they perform include rolling rocks; holding and carrying palm fronds with flippers; rolling in ropes and cables; climbing on, rubbing against, or rearranging logs; batting floats; and mouthing, sucking, or palpating a variety of objects. Often, manatees will hold objects with their flippers while mouthing them (165). Calves and juveniles can be "friendly" with boats by putting their flippers around or in them (168).

- *Interactions with Other Species*—Manatee interactions with other species are diverse. They associate with cows (34) and hippos, possibly to eat their feces (115). We reported above various instances of lifting or harassing alligators, which are ostensibly aggressive behaviors. The motivations for pursuit and manipulation of other animals, such as ducks, pelicans, turtles, and fish (175), are not clear, although observers suggest they are examples of play. Mike Birns (91) reports an interesting example of a manatee and juvenile Atlantic bottlenose dolphin (*Tursiops truncatus*) in Crystal River, Florida, batting the float from a crab trap back and forth.

- *Interactions with People* (178-184)—Interactions with people include a diverse, interesting, and at times entertaining (to people anyway) set of behaviors. Some of these behaviors suggest aggression such as in Monica Ross's report (178) of bumping behavior. Observers also report that manatees swim underneath people and lift them (29, 107, 110). Despite the fact that this behavior resembles the behavior shown toward alligators (71), a presumptive predator, it is considered play by several of our contributors (179). This dual interpretation is by no means out of the question. Consider metacommunications that dogs and other animals use to signal play before engaging in aggressive-appearing behavior (Wilson, 1975; Sutton-Smith, 1997). Perhaps manatees also employ metacommunication to signal a context for play.

  Another behavior akin to lifting is suggested by the following interaction with a boat. A large playful manatee put his face on the back of a kayak and pushed it 9.1 to 12.2 m quite fast (20). The same ambiguity is presented in this behavior as in lifting—is this an agonistic behavior or a friendly interaction? Some interactions with kayaks suggest masturbation or mating behavior (52, 98, 176).

  Interactions with human artifacts appear game-like at times, resembling a "keep-away" or "cat and mouse" type of behavior between conspecifics (93, 166, 180). Wayne Hartley describes an interaction between two manatees, "Donna" and "Doyle" (180): Donna was laying her head on a sock on the bottom. Doyle, another manatee, came up and grabbed the sock and swam off; he then stopped and looked back as if playing. Play-like behavior between a calf and people is suggested in an observation by Vincent Maida, who reported "playing" with a calf that would periodically swim back to its sleeping mother and then return to "play" some more (35).

  Other interactions suggest play-like behavior. Mike Birns (181) described an individual that liked to sneak up behind people and goose them. The higher they jumped and louder they squealed, the more "victory rolls" he did. This manatee was dubbed "Chester the Molester" for that and other behaviors. Grabbing behavior is described by other observers (25). Manatees sometimes grasp people with their flippers. Since this is an action that males do to females, perhaps the behavior represents a sexual interaction. Other behavior suggests some competitiveness for access to people (111) such as the fighting between two females for access to a male water guide discussed previously.

  At Crystal River, Florida, and other areas, Jennifer McGee (182) observed that if people are standing in water wearing flippers, manatees will often put their head on the flippers. Wayne Hartley described a similar event in Blue Spring, Florida, where four divers were standing, and a single manatee was laying on all their flippers (182).

  A series of interesting interactions between manatees and people are described by Lucy Keith-Diagne. The first involves vocalizations by calves swimming in the clear, warm-water discharge with ~200 other manatees at the Riviera Beach Power Plant in Florida. Keith-Diagne and an intern were standing in the water, chatting, when about six to 10 calves surrounded them. When they put their heads underwater, they could see the calves watching them and hear them chirping. One of them nuzzled her knee, backed up, and continued chirping with the others (183).

  A second example suggests some possibly iconic behavior (i.e., a transparent signal) by two young African manatees. An orphan calf and subadult African manatee made a gesture of putting their flippers to their mouths under

several different conditions. The orphan calf did it when he no longer wanted his bottle. The other instances were under circumstances that suggested the manatee was scared: the first as people entered the water and the second when the manatee was caught by the tail in a net (184). We have observed this flipper-to-mouth gesture by two male manatees at Mote Marine Laboratory (Bauer, pers. obs.). We interpreted the gesture as a "feed me" signal. Since these were two highly trained manatees, and the behavior occurred in a feeding context, we could not be sure we had not inadvertently trained the behavior.

The third anecdote describes observations of manatees in Senegal. These manatees approached people at the edge of rivers, interacted with women washing dishes or clothes, and played with swimming children (34).

Mimetic Behavior and Social Learning (185-189)—Some types of social learning can facilitate behavior acquisition and social interactions by reducing or obviating the need for slow trial and error learning, potentially accelerating adaptation to changing environments (Shettleworth, 2010). Manatees synchronously surf the waves generated by the opening of water control structures (Reynolds, 1981). They synchronously, although not necessarily simultaneously (185), rise to the surface to breathe (Hartman, 1979). They also breathe synchronously while swimming rapidly (186). Anecdotes from experienced observers report other examples of mimetic behavior, including learning the type and location of food by rehabilitated manatees after observing nearby wild manatees (187). Monica Ross and Nicole Bartlett (43) report a manatee escaping from a net capture by following another manatee.

Two other examples suggest different processes. In the first case, Mike Birns reports, "A female manatee swam toward me and stopped about a meter away, staring at me. My nose itched, and I scratched it with my right hand. Like a mirror, she rubbed her snout with her left flipper. I did it again to see if it was a coincidence, and she mirrored me again. So, I rubbed my nose with my left hand, and she put her right flipper to her snout" (188). This "do as I do" behavior appears to involve learning a novel behavior, an example of true imitation (Whiten & Ham, 1992) and apparent recognition of correspondence of dissimilar body parts (e.g., hand–flipper). This is a type of imitative behavior reminiscent of that reported for dolphins (Herman, 2002).

The second example does not initially appear to be quite as functional, which, given the young age of the manatees, suggested to Jim Reid that it might be play (189). Reid observed a sequence in shallow water (0.6 to 1.2 m) at Kennedy Space Center, Banana River, Florida. A subadult raised its head and flippers above the water and then slowly fell. These actions were followed by another manatee doing the same behavior. Over about a 15-min period, this behavior was repeated at least 10 times by five to six manatees. Some were in close proximity, but others were 15.2 to 30.5 m apart. The manatees apparently initiated their behavior by tucking their tails underneath them so that the paddle lay flat on the shallow shoal. The behavior appears to be coordinated, perhaps mimetic, but if so, how was the behavior communicated? At the distances indicated, acoustic transmission is suggested.

Discussion

We were surprised by the range and variety of behaviors revealed in this collection of anecdotes. Some of these may be one-time, aberrant events or perhaps misinterpreted actions, but others may be more broadly informative about manatee behavior. Interspecific association with a dolphin, playful and mimetic interactions with humans, male buddies, defensive behaviors against alligators and sharks, cooperative behavior, teaching-like behavior, responding to human song, navigating by dead reckoning, subtle motor actions to avoid objects, and visual tracking are just a few of the reported examples. Eating a rat adds to the already known variety of foods consumed by manatees. The narratives reported here and in the Supplemental Table may be known within the community of manatee field observers, but many are not represented in the literature where they might better generate productive research. These anecdotes can be integrated with current areas of research and, in some cases, suggest new lines of inquiry.

Manatees show a variety of responses to boats, which may reflect differences in species, environments, manatee activities, or individual traits. The anecdotes on anti-predator behavior might yield some insights to the degree that responses to vessels might be similar to responses to potential predators. Rycyk et al. (2022) have recently reported acoustic differences in local habitats that might affect responses to vessels through differential sound transmission, but more work remains to be done to explain manatee behavioral variability.

Manatee interactions with people require explanation. Some manatee actions, such as lifting, have a play-like character, but the fact that they show the same behavior with alligators makes motivational interpretation difficult. Explaining the variability in behavioral responses to boats and people will be important in establishing management regulations. Anecdotes of interactions

with people appear to be strongly subject to anthropomorphic interpretation, including attribution of mental states to manatees. One aspect of these anecdotes that may be fruitful to study is the range of individual variability, and the extent to which the same individual may exhibit a range of interactive behavior that depends on environmental variables that are observable.

Navigational abilities of manatees show considerable range—from the long-distance travels of a few individuals to the complex travel in nearshore coastal waters. The mechanisms involved in straight-line travel across open waters and intricate movement along shorelines, including travel in murky waters and at night, remain to be explored.

Our laboratories at Mote Marine Laboratory and the University of Florida investigated manatee senses. We surmised how their acute sense of touch (Reep et al., 2011; Gaspard et al., 2013, 2017) might be used, but the anecdotes on the evasive behavior in murky water or at night empirically support the idea that manatees can use tactile sensitivity, probably mediated by the constellation of sensory hairs located across the manatee body, to avoid objects. The specific parameters (e.g., detection, discrimination, identification) of this sense and its mechanisms can be studied in a controlled laboratory setting. Manatees' excellent hearing indicated by low thresholds, high-frequency detection, good sound localization, and low critical ratios (i.e., good hearing in noise) presumably underlies boat and people avoidance behaviors, and perhaps mother–calf and other conspecific vocal communication. Further research is needed on auditory constraints generated by ambient acoustical differences. Conflicting naturalistic reports on vision (e.g., tracking and visual recognition) and laboratory evidence suggesting limited visual abilities require future study to resolve. In addition, reports on manatees' ability to navigate under restricted visual conditions suggest the need for further study of chemical, thermal, magnetic, and gravitational senses (Horton et al., 2020).

Social behavior by manatees is particularly intriguing. They are putatively semi-social, but we have an anecdote on male manatee "buddies." Observer narratives describe a variety of social interactions, including mimetic, teaching-like, and play-like behavior among manatees and between manatees, and with people that suggest an unanticipated level of social cognition. These all suggest a need for further research.

Finally, the narratives suggest flexibility in such diverse areas as learning, food consumption, and navigation, which may contribute to solutions for conservation. For example, can manatees adapt to new locations and food sources? This area of inquiry has implications for moving manatees from sites that have become inhospitable. Given their apparent cognitive flexibility and good hearing, why are the same manatees repeatedly struck by boats? Studies of masking by multiple boats and the effects of the acoustical environment (e.g., Rycyk et al., 2022) are needed to address this question.

Although our participant narratives complement published literature in many ways, the most interesting feature revealed by these anecdotes is the flexibility of manatee behavior, a hallmark of intelligence. Managers and conservationists may be able to tap this behavioral diversity to enhance manatee health and survival in changing environments.

These are just a few examples of the research topics suggested by the observer anecdotes. We hope this generates additional research ideas from manatee researchers.

Supplemental Table

Anecdotes that are numbered in the text are referenced in the Supplemental Table. Most anecdotes pertain to Florida manatees (*Trichechus manatus latirostris*). Anecdotes pertaining to Antillean manatees are identified by (*Tmm*) – *Trichechus manatus manatus*, and those related to African manatees are identified by (*Ts*) – *Trichechus senegalensis*. We received no reports on Amazonian manatees (*Trichechus inunguis*). For the most part, anecdotes are listed under only one category to avoid repetition, but they may be applicable to other categories.

Note: The Supplemental Table for this article is available in the "Supplemental Material" section of the Aquatic Mammals website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.

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