The Elusive Manatee

An ethological approach to understanding behavior in the West Indian manatee

Antillean manatee in Belize 1999 Photo © Leszek Karczmarski

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PREFACE

This Species Brief originated in WFSC 422, an ethology course taught by my academic advisor, Dr. Jane M. Packard, at Texas A&M University in 1998. It was updated this year for distribution to Earthwatch Institute volunteers. ***Please consider it a work in progress – a "draft document" as it is continuously being revised and updated with better references and new information.*** Designed to be used by schools, zoos, wildlife parks, and oceanaria, it makes an excellent starting place for students, teachers, and others who are interested in learning about animal behavior and/or **sirenians** (manatees & dugongs). But, remember, it is only a briefing document. Use it to catapult yourself into the exciting world of animal behavior -- using manatees as an example. For more details, start with the **Recommended Reading** section; scientists and university students are encouraged to delve into the primary literature listed in the **References** section.

PART I: INTRODUCTION

As we idled around the corner of Swallow Caye I sighted two manatee noses in the distance. They were barely visible as they broke the surface of the clear Caribbean water. Patch, our boat operator, spotted the manatees at almost the same instant – he probably saw them first -- because before I could motion to him, he had already shut down the engine. We waited in silence, hoping they would surface again. So it goes with research on the elusive manatee. Most behavioral observations of manatees have been conducted on Florida manatees, either in captivity or in the clear spring waters of Florida during winter aggregations. Only recently have we attempted to observe behavior in Antillean manatees, which are sparsely distributed throughout the Caribbean, including the tropical waters of Belize.

Five minutes passed - how long can these guys stay down? What are they doing down there? One reason we know so little about these incredibly well adapted animals is because they spend the majority of their time underwater, regularly staying submerged 3-5 minutes between breaths. *We heard them before we saw them. Both noses broke the water with a forceful exhalation at virtually the same moment. Then they were down again. I quietly entered the water and stealthily snorkeled the 50 meters towards their last location. Where did they go? Stop. Look. Listen. I heard them breathe again. When they finally came into view underwater, I thought, "Uh oh... a mother calf pair -- they are going to run away".*

The larger animal was about 3 meters long, almost twice as big as the smaller. Readings and previous experience led me to assume a mother-calf relationship based on this size differential. *But they didn't run. The larger animal was gently nuzzling the smaller one's back with its big* ***prehensile*** *lips. The next time they surfaced to breath, they were nose to nose in a manatee "kiss". When they noticed us, the nuzzling stopped and they both sank slowly to the soft muddy bottom. As they sank, I heard a few squeaks, similar to manatee vocalizations I'd recorded between mother-calf pairs last year. There they rested, side by side in typical mother-calf position, for three minutes. When the smaller one rose to the surface to breathe, I could tell it was a female by the location of a genital slit near the anus.*

But, what a surprise I had when the larger animal surfaced and I saw by a genital slit near the umbilicus scar that it was a male. I'll make no more assumptions about mother-calf pairs based on size differentials!

Ethology

Do manatees breathe simultaneously? If so, why? Why was the large male manatee nuzzling the smaller female? Why do manatees "kiss"? How did they sink to the bottom and stay - without moving a muscle? Why did they vocalize during their descent? How do manatees create sound? Do manatees often lie side by side on the bottom? Are manatees usually found in pairs, or groups, or alone? Why? How long can manatees stay underwater without breathing? Why did the smaller animal surface to breath before the larger animal did? These are just a few of the questions raised by the brief observation. Some answers to these "how" and "why" questions are known; other answers may come through long-term ethological studies.

Ethology is a relatively new, multi-perspective scientific approach to the study of animal behavior. Made famous by the work of 1973 Nobel Prize winners, Konrad Lorenz, Karl von Frisch, and Nikolaas Tinbergen (www.nobel.se/medicine/laureates/1973/index.html), it focuses on animal behavior in a natural setting. By using a **Scientific Perspective**, it differs from **Folk Psychology**, which is often used to explain animal behavior to the general public. **Folk psychology** perspectives are intuitive in nature, usually based on personal experiences and observations. They are considered **anthropomorphic** because they describe and explain behavior in human terms – which are often the only terms we have to start with! These perspectives are appropriate and very useful when communicating with non-scientists, such as audiences in zoos, oceanaria, and wildlife parks. An interpreter will often use **folk psychology** to describe and explain animal behaviors based on the "model" that animals have desires, beliefs, and emotions like humans. Scientists also use these perspectives in developing hypotheses about specific behaviors. For example, I was using **folk psychology** when I assumed that the manatees in the **anecdote** above were a mother-calf pair. My intuition was based on the size differential and behavioral patterns typical of mother-calf pairs.

Ethology encourages us to develop additional **Scientific Perspectives** in understanding, explaining, and/or describing animal behavior; the classical ethological perspectives include **cause**, **development**, **evolution**, and **function** (Martin & Bateson 1993, Lehner 1996). Modern ethologists agree that the behavior of an animal is the result of complex interactions between the genetic makeup of an **individual** and environmental factors that act upon the **individual** (Alcock 1998). However, many aspects of an animal's behavior can be explained from two very different perspectives: **proximate** and **ultimate** (Martin and Bateson 1993, Lehner 1996). This often results in miscommunication among observers who are looking at behavior from different perspectives. **Proximate** and **ultimate** comparisons are equivalent to apple and orange comparisons – i.e. they are both valid fruits, but they are different things. "How" questions are usually asked from a **proximate** perspective; how questions seek explanations about the physical and chemical mechanisms that trigger an **individual** animal's behavior at any given point in time. "Why" questions, on the other hand, are usually based on **ultimate** perspectives; answers to these questions attempt to explain why certain behaviors exist within a **population** (or species) of animals. In other words, what pressures of **natural selection** led to the existence of a particular behavior within a **population** or species. Ethologists further divide **proximate** and **ultimate** into the sub-categories of **cause**, **development**, **evolution**, and **function** based on the work of Niko Tinbergen (Martin and Bateson 1993, Lehner 1996).

Proximate: **Cause** and **Development** are **proximate** perspectives, which look at the behavior of an **individual** animal. **Proximate Cause** perspectives include looking at both internal mechanisms (hormones, neurotransmitters) and external stimuli (pheromones, photo-period, temperature) that interact to trigger specific behaviors in a mature animal. Dr. Jane M. Packard explains it using the analogy of a camera, "Think of **Proximate Cause** as a snapshot in time that shows what is causing the behavior at that particular moment." For example, in our observation above, what "caused" the manatees to kiss? Was the female was giving off some signal (vocal, chemical, or behavioral) that attracted the male? Did the tactile stimulation by the male cause hormone production in the female, which triggered the "kiss"? Most likely, it was is a complex interaction between both the internal state of each animal and the resulting external behavioral stimuli. **Proximate Development** perspectives look at behavioral changes that occur as an individual animal matures. Think of **Proximate Development** as a "video" that shows how a behavior develops and changes over time as an **individual** animal matures. How might the behavior of manatees at different ages compare to the interactions we observed?

Ultimate: **Evolution** and **Function** are **ultimate** perspectives, which look at specific behaviors present in a **population** of animals. These behaviors are thought to have evolved over time through the process called **Natural selection**. For **Natural selection** to act on a behavioral characteristic, the behavior must meet certain criteria – the same criteria necessary for **natural selection** to act on a physical trait such as coloration: (1) the trait must vary among **individual**s within a **population**; (2) the variation must be heritable; (3) if the heritable variation results in differential fitness (i.e. variations in the trait result in some **individual**s reproducing more successfully than others);

then (4) we would expect the behavior to become genetically fixed in the **population** as the proportion of **individual**s displaying the trait increased (i.e. changes in the proportion of genotype and resulting phenotype).

Ultimate Evolution perspectives include the comparison of behaviors among different, closely related species. This is our "video" perspective. From an **Ultimate Evolution** perspective, we hypothesize about how a behavior has changed (or remained the same) at the **population** and/or the species level over many generations. In my study of Antillean manatees, I will be comparing behavior to previous observations of behavior in Florida manatees. Although these sub-species are very closely related, they share different habitats. The Florida manatee inhabits a temporal/sub-tropic region where its behaviors are shaped by dramatic changes in water temperature during the year. On the other hand, the Antillean manatee inhabits a tropical region where the water temperature is relatively constant year round. We expect some behaviors to differ between the two sub-species as they evolved in different habitats. If behaviors, which we think are driven by water temperature today, exist in both sub-species, then perhaps they had some other **function** in the past.

Ultimate Function perspectives attempt to explain what the **function** of a specific behavior is within a **population**, (i.e. why animals that display this behavioral trait are more reproductively successful than **individual**s who do not). This is our "snapshot" perspective. If variation exists within the behavior, **Ultimate Function** is the perspective used to explain why. Some Florida manatees travel long distances into more temperate regions during the summer months while others stay in the same area year round – but we are not sure why the traveling behavior exists. The traveling animal must use more energy than the year round resident. Perhaps male animals that travel are exposed to more potential mates – thereby increasing their reproductive success. Chessie, a famous male manatee first sighted in the Chesapeake Bay in 1994, is known to have traveled between Florida in the winter and Rhode Island in the summer of 1995! Sweet Pea, a female rescued near Houston, Texas, later traveled along both coasts of Florida. Gina, a female manatee first sighted in Tampa Bay on the west coast of Florida is currently hanging out in the Bahamas! One of my questions is: Do Antillean manatees exhibit similar long distance traveling behaviors?

Hypotheses about "why" these behaviors exist in manatees are different from hypotheses about "how" these behaviors are executed. The "why" questions are from **ultimate** perspectives of **evolution** and **function**, the "how" questions are from **proximate** perspectives of **cause** and **development**.

We can remember the concepts of ethology with the acronym **AB=CDEF** (**Animal Behavior = Cause, Development, Evolution, Function**). On the TIME axis, **Cause** and **Function** are "snapshot" perspectives that look at internal state and external stimuli in an **individual** animal or at reproductive success in a **population** of animals. **Development** and **Evolution** are "video" perspectives that look at changes in behaviors over time, either as the **individual** animal matures or as the **population** evolves. On the ANALYSIS axis, **Cause** and **Development** are **proximate** perspectives that attempt to answer "how" questions at the level of **individual** animals. **Evolution** and **Function** are **ultimate** perspectives that attempt to answer "why" questions at the level of **population**s and/or species. For more information on Ethology, I encourage you to visit Dr. Packard's website: http://www.tamu.edu/ethology/. The four basic concepts of ethology can be arranged in a 2 x 2 table comparing TIME FRAME and ANALYSIS PERSPECTIVES (Table © Jane M. Packard).

TIME/ ANALYSIS	Pattern-Static "Snapshot"	Process-Dynamic "Video"
Proximate Perspective **Individual** Animals "How Questions"	**CAUSE** **(control)** behavioral triggers: internal state/ external stimuli	**DEVELOPMENT** **(ontogeny)** changes in behavior as an animal ages: maturation and/or learning
Ultimate Perspective **Populations/** Species "Why Questions"	**FUNCTION** adaptive significance: effect on reproductive fitness	**EVOLUTION** **(phylogeny)** changes in behavior (genotype) as **population**s/ species diverge

Sirenians

So what are manatees anyway, and why should we study their behavior? Manatees belong to the order **Sirenia** of which there are only 4 **extant** species in 2 families, Trichechidae and Dugongidae. Although scientists often lump **sirenians** together with the order **Cetacea** (whales and dolphins) as totally aquatic marine mammals, manatees and the dugong are actually more closely related to elephants, hyraxes, and aardvarks than to any other marine mammal (Fischer 1990, Maluf 1995, Springer et al. 1997, Gaeth et al. 1999). Until a few years ago, very few people had ever heard of manatees, dugongs, or sea cows. But, as we learn more about these elusive and highly specialized creatures that share our coastal habitats, they are becoming more and more popular among both scientists and conservationists. The West Indian manatee (*Trichechus manatus*), the West African manatee (*Trichechus senegalensis*), and the Amazonian manatee (*Trichechus inunguis*) are members of the family Trichechidae. The dugong (*Dugong dugon*) is the only surviving member of the family Dugongidae (Reynolds and Odell 1991).

Steller's sea cow (*Hydrodamalis gigas*) is usually included when we talk about modern **sirenians**; it was in the family Dugongidae (Reynolds and Odell 1991), but the species was **extirpated** by humans in 1768, just 27 years after it was discovered by Russian explorers in 1741 (Stejneger 1887). Today, local and international laws protect all four living species, but they are also either threatened or endangered by humans wherever they exist.

Florida Manatees: There is little evidence that Florida manatees were ever harvested commercially. But subsistence use, habitat destruction, and competition for space with recreational boaters have taken their toll on both prehistoric and modern **population**s. The USGS **Sirenia** Project, the U. S. Fish and Wildlife Service, and the Florida Fish and Wildlife Conservation Commission (formerly the Florida Department of Environmental Protection) have funded much of the manatee research in the United States. Over the past three decades, conservation efforts in Florida resulted in significant scientific research on the distribution, **population** biology, and behavior of the Florida manatee subspecies, *T. m. latirostris* (see O'Shea *et al.* 1995). Ecological and behavioral studies on localized **population**s such as those in Crystal and Homosassa Rivers (Hartman 1979), St. John's River (Bengtson 1981), and Sarasota Bay (Koelsch 1997) have added to our understanding of Florida manatee behavior. However, relatively little research has been conducted outside of Florida. Therefore, most of the referenced information contained herein refers to the Florida subspecies.

Antillean Manatees: Even before Russian sailors were exploiting Steller's sea cow meat in the North Pacific, European explorers were provisioning their ships with Antillean manatee meat from the Caribbean area. Besides harvesting manatees for subsistence, some Native Americans also sold manatee meat to the Europeans (O'Shea 1994). Today, the Antillean subspecies, *T. m. manatus*, is classified as endangered throughout its sparse distribution in the Caribbean Sea and Western Tropical Atlantic Ocean (Lefebvre et al. 1989). O'Shea and Salisbury (1991) suggest that Belize (formerly British Honduras), where manatees have been protected since the 1930s (Auil 1998), may be the last stronghold for Antillean manatees in the Caribbean. Current research in Belize by James A. "Buddy" Powell, Nicole Auil, Greg Smith, Katie LaCommare, and myself is expanding our knowledge of the Antillean manatee. Most of the **anecdotes** included in this brief come from my personal experiences in Belize.

PART II: PROBLEM-SOLVING

One way to interpret animal behavior is as a method of problem solving. Over geological time, animals have evolved behaviors that enable them to solve problems. Some of these behaviors are identical from one **individual** to another. We describe such a behavior as a Fixed Action Pattern (FAP), because the **individual**'s genes control the trait. In other words, the genetic trait has become fixed in the population and all **individual**s perform the behavior in exactly the same way because they inherited the trait from their ancestors. At the other end of the behavioral scale, we find behaviors that vary a great deal among **individual**s. We describe such a behavior as a Variable Action Pattern (VAP), because the environment controls the trait. In other words, each **individual** performs the behavior differently due to different environmental factors during development. Additionally, any **individual** may perform the behavior differently at different times, depending its internal state (hormones, chemicals, neurons) and on external stimuli (environment). Of course FAP and VAP are not specific categories, but are the end points along a continuum. If a behavior falls near the middle of this continuum, we describe it as a Modal Action Pattern (MAP). In other words, the behavior is controlled in part by genetics and in part by the environment.

We can divide problem solving into three major categories: reproductive, physical, and **social**. Manatees have evolved some interesting behaviors to overcome reproductive and physical problems. But, they are not considered to be very **social animals**. Although they tend to aggregate on resources, they do not appear to live in **social** groups and significant **social** behaviors have not been observed outside of reproductive activities. This species brief will use the concepts of ethology to introduce you to the behavioral methods manatees use to solve some of their reproductive and physical problems. We will examine specific behaviors using the different perspectives of **proximate** cause, **proximate development**, **ultimate evolution**, and **ultimate function** to answer a few questions regarding "how" and "why" manatees behave as the do.

Reproductive Problem Solving

*We idled into one of my favorite coves at the end of **Bogue** C in the Drowned Cayes near Belize City. I had taken volunteer researchers to this spot on previous occasions and ALWAYS, there had been a manatee resting in the **manatee hole** on the far side of the cove. As if on cue, before we could even cut the engine and anchor the boat, a single manatee surfaced in the vicinity of the **manatee hole**. Within minutes a second manatee surfaced in the middle of the cove. Two minutes later, a third animal entered the cove. "Gee..." I thought, "This must be a popular resting cove!" But, the two animals in the center of the cove were too active to be resting. I didn't think they could be feeding, either, because previous habitat snorkels had found NO vegetation on the bottom. Another four minutes passed and two more manatees swam under the boat to join the active pair in the middle of the cove. "This is great," I told the volunteers, "we'll be able to see how long it takes them to settle into a resting pattern". But they didn't settle.*

For the next hour we watched the four manatees in the middle of the cove breathe, roll, dive, and kiss while the first animal appeared oblivious to all the activity less than 50 meters away. Were we observing a **mating herd**?

Female Florida manatee nurses two calves. Photo © Florida FWCC

Mating System: One parameter of the West Indian manatee **mating system** is known as the **mating herd**. A **mating system** is the species-typical pattern of problem solving that includes how an **individual** finds a mate, how long it remains with the mate, and how much energy it invests in its offspring (Drickamer, et al. 1996). The West Indian manatee **mating system** can be broadly defined as **promiscuous** with the **estrous** female exhibiting **polyandrous** behavior and the male exhibiting **polygynous** behavior (Hartman 1979). A manatee-**mating herd** consists of a group of males in pursuit of an **estrous** female. The group is **ephemeral**, lasting only from a week to a month (Hartman 1979) and consisting of up to 20 males. The group does not remain together afterwards. Males will participate in multiple **mating herd**s and attempt to copulate with many **estrous** females; similarly, females will copulate with multiple males among those in the herd. When we discuss why this **mating system** exists in manatees, we are using the **ultimate function** perspective.

From the perspective of **proximate cause**, we do not know exactly what external signal stimulates males to aggregate around and attempt to copulate with the **estrous** female. Females must produce some sort of signal, possibly a chemical or acoustical signal, which stimulates an internal hormonal mechanism in males causing them to pursue her. Likewise, the male's internal state must be such that he responds to the signal. **Proximate development** perspectives would look at how the males' reaction to such a signal might differ at other stages of maturity.

Daniel S. Hartman, one of the first scientists to make long-term observations of manatee behavior in the wild, found similarities between manatee **mating herd**s and elephant mating, noting that female elephants are also **polyandrous** - often mating with several males over a period of several hours. When Hartman (1979) compares the mating behavior of manatees to that of elephants, he is writing from an **ultimate evolution** perspective. In other words, he is hypothesizing that this aspect of the **mating system** evolved millions of years ago in an ancestor shared by both the manatee and the elephant. Since **sirenians** and proboscideans are two of only four **extant** orders that share a common ancestor among them, manatees are often compared to elephants using the **ultimate evolution** perspective [NOTE: The other two orders contain the hyraxes and the aardvarks, which are rarely compared to manatees in the literature]. Another **promiscuous** aspect of the manatee **mating system** is **scramble-polygyny**, where multiple males attempt to mate with the **estrous** female, but - without overt competition. Although males aggregate on the **estrous** female and jockey for the best position - they exhibit little **agonistic** behavior. Interestingly, male dugongs appear to be more **agonistic** during mating events. They set up territories and exhibit **lek** mating behaviors (Anderson 1997). What perspective would we use to compare mating strategies between manatees and dugongs?

Timing: Let's assume that our observation was of a **mating herd**. That is, the group of manatees in the center of the cove consisted of 1 **estrous** female and 3 males. Why was the first manatee, the one originally sighted in the resting hole, not involved in the **mating herd**? Looking at the situation from a **proximate** perspective, there are several possibilities, and all involve timing. Suppose the resting manatee was a female. If she was sexually mature, but not in **estrous**, the **mating herd** would have no interest as she would not be producing an **estrous** signal. An **estrous** signal is the **proximate cause** of the **mating herd** behavior. It's "how" the males know the female is ready to conceive. Similarly, if the female were sexually immature, she could not be in **estrous** and therefore would not be sending a signal. Scientists have only recently answered the question of when a female manatee becomes sexually mature, thanks to the development of a new aging technique by Miriam Marmontel, et al. (1990). Since manatees continuously regenerate new teeth throughout their lives (Domning and Hayek 1984), they cannot be aged by their dentition like many other marine mammals. But, by looking at growth layers in manatee ear bones, we are now reasonably confident that female manatees in Florida reach sexual maturity between the age of 3 and 4 years - most giving birth to their first calf at age 4 (Marmontel 1995). Questions of "how" the behavior of signaling develops in females as they mature fall under the **proximate development** perspective.

On the other hand, if the resting manatee was a male, why wasn't he attracted to the **estrous** female in the middle of the cove? He could have been either sexually immature or sexually inactive. Using the presence or absence of sperm in the testes as an indicator, Hernandez et al. (1995) found that sexual maturity (**proximate development**) varied among Florida male manatees with both size and age with

some males becoming physiologically mature as young as 2 years and as small as 237 cm. But, from a **proximate cause** perspective, they also found that the reproductive system varied in functionality among mature male manatees depending on season in Florida, with little evidence of spermatogenesis present during winter months (December – February). In many mammals, reproductive activity varies seasonally with photoperiod, or the number of light hours per day. The pineal gland is usually the organ associated with behavioral changes affected by photoperiod. However, no pineal gland has ever been found in manatees or dugongs (Ralph et al. 1985, W. Welker personal communication 2000). From an **ultimate evolution** perspective, it is interesting that the literature is unclear regarding the existence of a pineal gland in elephants (Ralph et al. 1985).

Whether the resting manatee was inactive or immature, his timing would have been out of sync with the female and the **estrous** signal would have no effect on his behavior. From an **ultimate function** perspective, we say that those manatees whose sexual behavior is triggered at the appropriate time (i.e. when both the male and female are sexually mature, active, and receptive) are more reproductively successful than manatees that waste energy on futile sexual encounters. From an **ultimate evolution** perspective, there have been some behaviors observed in Antillean manatees that might be associated with seasonal spermatogenesis (G. Smith unpublished data). More studies are necessary before we can determine if seasonality affects the reproductive behavior of manatees in Belize.

Parental Care: The final aspect of reproductive problem solving discussed here is parental care. Like many mammals, female manatees invest considerable time and energy into a relatively small number of offspring as their reproductive strategy. From an **ultimate function** perspective, data collected by scientists in Florida suggest that those females that invest 2 years of parental care in each offspring prior to becoming pregnant again are more successful than other females (Marmontel 1995). Although calves begin eating on their own within 3 months of birth, they continue to nurse periodically (Hartman 1979) as they grow and learn migration routes from their mothers (R. Bonde, personal communication 1999). When we ask "why" this behavior exists, we are asking **ultimate function** questions. Perhaps calves need the extra protein and fat provided by mother's milk during developmental years. Or, perhaps it takes calves almost two years to learn the routes to warm water effluents and good foraging grounds necessary for survival through the temperate winters in northern and central Florida.

In an ongoing study of Antillean manatees in the Southern Lagoon of Belize, Buddy Powell is also seeing mother-calf pairs remain together for long periods of time (www.wesave.org/manatee/). When we compare this behavior between the Florida and Antillean subspecies, we are using the **ultimate evolutionary** perspective. On the other hand, "how" the mother-calf pair remains together during this period is a **proximate cause** question. It appears that calves remain in close association with their mothers via vocalizations (Hartman 1979; Reynolds 1981; Bengtson and Fitzgerald 1985; personal observations).

Although manatees usually have only one calf at a time, there are rare occurrences of manatees giving birth to twins (Hartman 1979; O'Shea and Hartley 1995; Rathbun et al. 1995). Twinning is often followed by the death of one (O'Shea and Hartley 1995) or both (L. Lefebvre, personal communication; personal observation) offspring. From an **ultimate function** perspective, this alternative behavior raises the questions (1)"why" aren't females that have twins more successful than those that have singles?" and (2) "why has the variation (single vs. twins) in birthing behavior persisted within the West Indian manatee?" From an **ultimate evolution** perspective, the variation could be studied by looking at closely related species. Unfortunately, there are little data available on the occurrence of twins within other manatee species, but Marsh (1995) references vague reports of twin fetuses in dugongs. This is one line of evidence that twinning is a characteristic shared with other **sirenians** and not recently derived within the Florida **population**.

Before we leave parental care, we should ask, "could the observation described in the introduction have been a manatee father caring for his offspring?" Probably not, there is no evidence that male manatees participate in any form of parental care. A better hypothesis, based on what we now know about manatee reproductive behavior, is that perhaps the large male was attracted to little female because she was sending an **estrous** signal.

Summary: We have learned much about Florida manatee reproductive strategies over the past three decades. Studies on free-ranging manatee **population**s at warm water effluents and data collected from carcasses through the salvage network agree on many life history traits (O'Shea et al. 1995). Female manatees appear to reach sexual maturity at age 3, producing their first calf at age 4. Single births are the norm with rare cases of twins. More twins are reported in carcasses than observed in live manatees, leading to the assumption that **uniparity** is the more successful behavior. **Gestation** is about 1 year and calves stay with their mothers for about 2 years, making the minimum interval between successful reproductions about 3 years. However, females who abort fetuses or lose a young calf may reproduce again sooner. Florida males exhibit seasonal spermatogenesis, which correlates with seasonal observations of females with **neonate** calves.

Physical Problem Solving

Sirenians (manatees and dugongs) belong to group of animals commonly referred to as marine mammals. Other marine mammals include whales and dolphins; seals, sea lions, and walruses; sea otters; and polar bears. Although they are not closely related to each other (remember, manatees are more closely related to elephants than to other marine mammals), these groups share **convergent** characteristics that evolved as they solved the physical problems associated with adaptation from a terrestrial to a marine environment. For example, all marine mammals must breathe air, and they have evolved in various ways that enable them to survive in an aquatic environment. In the dolphins, nostrils have migrated up the rostrum to the top of the head and become a single blowhole. Many large whales and seals have physiological adaptations that enable them to remain underwater for hours at a time.

From an **ultimate evolutionary** perspective, one interesting hypothesis is that the common ancestor between manatees and elephants was an aquatic (rather than a terrestrial) mammal. If true, this would make the elephant the only known animal to move from the sea to the land (as all mammal ancestors did when their remote ancestors evolved from fish to amphibians), back to the sea (as did the cetaceans, **pinniped**s, and **sirenians**) and then back to the land again. This idea was originally based on the thought that the elephant's trunk evolved to enable the negatively buoyant animal to breath air from beneath the surface of the water. The longer the **proboscis**, the deeper the animal could forage - eventually resulting in the long, snorkel-like trunk we see today. This hypothesis has recently been supported by a study on elephant embryos, which indicates that the shared ancestor between **sirenians** and elephants was an aquatic mammal (Gaeth et al. 1999).

All marine mammals have had to solve the problem of breathing in an aquatic environment, but the **sirenians** have additional unique physical problems: (1) the **extant** species are NOT well adapted to cold water; and (2) **sirenians** are the only marine mammal **herbivores**. Only one **extinct** species of **sirenian** was found in extreme cold waters: *Hydrodamalis gigas*, commonly known as Steller's giant sea cow. These animals were three times as large as manatees, ranging from 25 to 35 feet in length and weighing up to 8000 pounds. Their extremely large size enabled them to survive in the frigid Bering Sea where they feed on giant kelp. All **extant** species of **sirenians** are limited to tropical and sub-tropical waters year round; some **individual**s migrate into temperate areas during the summer. As **herbivores**, all **sirenians** are limited to shallow coastal waters, estuaries, and rivers where aquatic vegetation is abundant. The West Indian manatee inhabits riverine and marine systems from Florida to Brazil. But their distribution is patchy, and appears to be a **function** of physical problem solving such as **thermoregulation**, **foraging**, **predator** avoidance (Hartman 1979), and **osmoregulation**. These are the problems we will focus on here.

Thermoregulation: Water temperature is well known to be a controlling factor in Florida manatee distribution in the United States (Hartman 1979, Irvin 1983). Rarely, manatees have been sighted in North Carolina (Schwartz 1995); they are routinely sighted in South Carolina and Georgia; but the Chesapeake Bay has always been considered north of any expected range - even in the summer. Chessie, a male Florida Manatee, earned his name by showing up in the Chesapeake Bay during the summer of 1994. **Sirenian** biologists agreed that Chessie would die from the cold of oncoming winter if he remained in the Bay, so they flew him back to Florida, put a satellite transmitter tag on him and let him go. When the water began to warm the next summer, Chessie headed north again. Not only did he temporarily enter the Chesapeake Bay, but when he came out, he continued his northern journey up the Atlantic seaboard. Upon reaching Port Judith, Rhode Island, he finally reversed direction and began working his way back to Florida for the winter! [For more details go to www.sirenian.org/chessie.html]

Each winter, hundreds of West Indian manatees aggregate in Crystal River, Florida, where they are soon joined by thousands of humans who want to swim with them. Why does the otherwise elusive manatee tolerate this human behavior? Why do they keep coming back, year after year?

These are excellent examples of how manatees have adapted behaviors to solve the physical problem of thermoregulation. While most marine mammals have adapted to cold water by evolving high metabolic rates, the West Indian manatees have exceptionally low metabolic rates (Irvin 1983). When metabolic rates are graphed against body size, most mammals fall along a predictable curve where the rate decreases as the size increases. If we compare where manatees should fall on this curve to where they actually plot out on the graph, we find that manatee metabolism is only about 20% of what we would expect. The same comparison with other marine mammals shows that their metabolic rates are almost twice what we would expect - enabling them to easily live in cold water. This physiological problem should limit the West Indian manatee to warm tropical waters.

In the United States, however, the Florida subspecies **thermoregulate**s behaviorally by migrating to both natural and artificial warm water effluents during the winter months, enabling them to extend their habitat range. From a **proximate cause** perspective, the migration behavior is triggered when the water temperature drops below 20 degrees Celsius (Hartman 1979; Irvin 1983). But, from a **proximate development** perspective, how do adult manatees know where to find warm water effluents? We touched on this earlier, when we talked about why manatee

calves remain dependent on their mothers for up to 2 years. Long term studies of radio tagged females with calves indicate that manatees initially learn migration routes from their mothers during the extended parental care period (R. Bonde, personal communication). Because of this learned behavior, interruption of man-made thermal effluents may have negative impacts on manatee survival in areas where no natural warm water effluents are nearby (Packard et al. 1989).

What about manatees in tropical habitats where water temperatures are relatively constant? If thermoregulation were the only **function** of long distance travel, we would not expect Antillean manatees to exhibit the same degree of seasonal migration as Florida manatees. Buddy Powell (personal communication 2000) is working on that **ultimate evolution** question through telemetry studies of Antillean manatees in Belize (see Satellite Tracking of W.I. Manatees in Belize www.wesave.org/manatee/). After almost two years of data, it appears that several manatee mother-calf pairs remain in the Southern Lagoon area year round. On the other hand, Greg Smith (personal communication) finds male manatees seasonally absent on the reef at Basil Jones, Ambergris Caye, during the winter months of December - February. In my limited personal observations, I have not observed manatees on the reef at Gallows Point Reef, near Belize City, from November through April; but they were there daily in July and August 1999. Temperature changes between summer and winter on Gallows Reef vary from about 28 – 32 degrees Celsius (unpublished data), well above the 20 degree trigger found in Florida manatees. If temperature is not driving this apparent seasonal migration, what other factors could be the cause? Greg Smith hypothesizes that it is driven by seasonal reproductive cycles. Perhaps the males "hang out" at the reef during the summer months looking for an **estrous** female (see previous section on reproductive problem solving). More data are required before we can answer these questions.

Foraging: *As we explored the **bogues** (channels) that snake their way through the mangrove islands off the coast of Belize, it became apparent that Antillean manatees preferred certain micro-habitats within the larger habitat we call the Drowned Cayes. We reliably found manatees just west of the cayes feeding on turtle grass beds; and we always found manatees resting in narrow **bogues** or quiet coves among the cayes. They tended to travel in the deeper channels when moving between areas.* One of the parameters of quality manatee habitat is the close availability of food (Hartman 1979). It appears that Antillean manatees using the Drowned Cayes are more likely to rest in areas that are linked to turtle grass beds by deep channels. Like all **sirenians**, manatees are opportunistic **herbivores**, feeding on a variety of fresh and saltwater vegetation. Although they may consume fish in some areas (Powell 1978) and incidentally ingest invertebrates (Powell 1978; Powell 1984; personal observations), the main component of their diet is aquatic vegetation: sea grasses in the marine and estuarine environment; floating, submerged, and emergent plants in the riverine environment. Sea grasses, like all plants, require sunlight for growth, which limits their presence to relatively shallow coastal waters. From an **ultimate function** perspective, the relationship between sea grasses and water depth has probably prevented manatees from dispersing into deeper oceanic waters.

I snorkeled up to an Antillean manatee feeding underwater just west of Swallow Caye – at first, I thought it was dead... I can still recall the adrenalin rush as options flashed through my mind regarding what to do with a dead manatee! It was lying perfectly still on the bottom in about 3 meters of water and appeared to be missing its head. As I floated closer, (heart racing) I began to hear chewing noises and realized that the manatee had buried its head into the muddy substrate and was feeding on the sea grass roots. I soon learned that this is typical of how manatees feed on the sea grass beds near the Drowned Cayes - eating both roots and leaves and probably other benthic organisms living in the mud. Looking for muddy disturbances became another method of finding the elusive manatee.

If you've ever tried to dive down and recover a lost item in deep water, you know that you, like most mammals, are positively buoyant and must work to get and stay submerged. Manatee bones are pachyostoic -- very dense and lacking marrow -- except in the vertebrae and sternum (Odell and Reynolds 1991). Because of this, manatees are negatively buoyant and can lie on the sea bottom without exerting any energy to stay down. The less energy they use, the longer manatees can remain submerged between breaths - making feeding more efficient. Indeed, we think manatees have the ability to control the volume of air their lungs, enabling them to rise to the surface, take a breath, and return to the bottom with no noticeable effort.

Manatees exhibit different problem-solving behaviors related to foraging in different habitats. In rivers, manatees are often observed feeding on floating vegetation. They use their forelimbs like we use our hands to manipulate aquatic plants towards the mouth. The large **prehensile** upper lip is then used to work the plants into the mouth. When I was observing Georgia and Peaches in Florida, I was fascinated to see Georgia reach her head out of the water to feed on plants growing along the shoreline of the Hontoon Dead River. At times it looked as if she was going to climb out onto the bank! In fact, Florida manatees feeding on grasses have been sighted with up to one third of their body awash (Powell 1984).

Although they are considered opportunistic feeders, manatees are known to prefer certain species of plants to others (Bengtson 1981). Hunters of West African manatees use cassava to lure the animals into box traps (O'Shea

1994). Other traditional hunters attract manatees by dangling a favorite flower over the water's edge to entice their approach. While West Indian manatees in Florida and Belize feed on a variety of vegetation including floating, submergent, emergent, and over-hanging vegetation, the Amazonian and the West African manatees feed primarily on surface vegetation.

In Gambia, when feeding on overhanging vegetation, West African manatees grasp the leaves of branches with their lip pads near the water's surface (Powell 1984). They pull the branch into the water; use their forelimbs to hold it down; and then eat the leaves - but not the woody petiole or branches. They appear to prefer the young leaves and shoots of mangroves, as they are known to return to areas where they have previously fed to crop any new growth. Amazonian manatees face an even more challenging problem. During the rainy season, floodwaters allow manatees to literally "forage among the tree tops", but in the dry season, they are often confined to isolated lakes and pools devoid of any vegetation. Robin Best calculated that Amazonian manatees could fast for up to seven months a year - surviving on stored fat reserves they build up during the rainy season (O'Shea 1994).

Daryl Domning of Howard University describes morphological variation in the rostrum deflection among manatee species and subspecies and suggests that the variation results from differential foraging behavior among **sirenian** species (1980). For example, the rostral deflection in both the Amazonian and the West African species is relatively less than it is in the West Indian manatee. These comparisons of foraging behavior and rostral deflection represent **ultimate** perspectives. Comparing foraging behaviors among the species is an example **of ultimate evolution**. Hypothesizing about why the rostral deflection varies among species (because of different foraging behaviors) is an example of **ultimate function**. From an **ultimate** perspective, it is interesting to compare the foraging behavior of manatees to the dugongs. Dugongs forage exclusively on submerged marine sea grasses and their rostra are significantly deflected downward when compared to manatees. The divergence in foraging behavior between the two families of **Sirenia** may be due to the **evolution** of true grasses in the Caribbean and continuously regenerating teeth in manatees. Unique to the *Trichechus* genus, is the fact that manatees generate new molars throughout their lifespan (Domning and Hayek 1984). As older molars are worn down from the abrasive silica content in true grasses, new molars gradually move forward at the rate of a few millimeters per month. The forward most molars eventually fall out and are replaced from the rear in a horizontal manner. This would be analogous to humans continuously generating new wisdom teeth at the rate of four - 2 lower and 2 upper - every few months! Daryl Domning (1982) convincingly argues that this trait enabled manatees to out compete dugongs in the Atlantic a few million years ago. While manatees are only found in the Atlantic and continue to forage on a variety of vegetation, dugongs are only found in the Indo-Pacific and forage exclusively on marine sea grasses.

Predation: Although they may have existed in the past, we know of few natural predators on modern West Indian manatees...EXCEPT for humans. Large aquatic predators (crocodiles, alligators, sharks, and hippopotamus) have been hypothesized to take the occasional small or weak animal (Odell 1982; Powell 1984). But, in one of the few documented cases, Johnson (1937, as reported in Powell 1984) found that only one out of one hundred crocodiles cut open contained the remains of a manatee.

Amazonian manatees, on the other hand, still have to contend with predation by aquatic and terrestrial carnivores such as jaguars, caimans, and sharks (Reynolds and Odell 1991) – especially during the dry season when then are stranded by receding flood waters. Both fossil and historical records indicate that manatees have been hunted both for subsistence and commercially throughout the history of humans (Lefebvre et al. 1989, Reynolds and Odell 1991). While illegal poaching still exists – especially in remote areas -- most modern predation is incidental – resulting from entanglement in fishing gear, shark nets, and water control devices, and from collisions with watercraft. From an **ultimate function** perspective, we may hypothesize that the reason manatees are elusive creatures is to avoid predation. In other words, those animals that inherited a natural tendency towards elusive behavior were more reproductively successful.

The story of Steller's sea cow demonstrates how quickly humans can extirpate a species, particularly when **population** numbers are already reduced. The sea cow was discovered and described by Georg Wilhelm Steller, a German naturalist assigned to Captain Vitus Bering during a Russian Expedition to Alaska (Steller 1988). This giant **sirenian** was 25-35 feet long and weighed ~8000 pounds with flukes than spanned 8 feet. Unlike modern **sirenians**, it lived in extremely cold waters in the North Pacific. It had no teeth, but two grooved plates - one upper and one lower with which it crunched giant sea kelp. During the summer of 1741, Captain Bering set sail from Kamchatka in NE Russia with 2 ships, the St. Peter and the St. Paul. During the voyage, a storm separated his ships; Bering, Steller, and the crew of the St. Peter were shipwrecked on an unknown island (later named Bering Island). Although Bering did not survive the winter, Steller and many of the crew did. In his book, A Voyage with Bering, Steller credits their survival to the giant sea cow. Only after the crew learned to hunt the sea cow did they begin to regain the strength to repair their ship. When they returned to Kamchatka in the summer of 1742, they told of the wonderful sea cow meat. New hunting expeditions were formed almost immediately and every year thereafter. The expeditions would return to Bering Island where they spent 8-9 months hunting fur-

animals and eating sea cow meat to survive. Indeed, many of the expeditions are reported to have wintered on Bering Island for the express purpose of collecting sea cow meat to provision their ships for the rest of their 3-4 year voyage to America. As a result, the last sea cow was reported killed in 1768, only 27 years after modern humans had discovered the island and the species.

Even before Russian sailors were hunting Steller's sea cow to **extinct**ion, European buccaneers and explorers were provisioning their ships with Antillean manatee meat, which they harvested themselves or purchased from the indigenous people (Reynolds and Odell 1991). In the Panama area, it is estimated that at one time, 7-8 thousand manatees were being harvested annually. The Amazonian manatee continued to be commercially harvested for it's tough skin (which was made into leather products) into the 1950's. From an **ultimate function** perspective, it stands to reason that manatees that behaved in an elusive manner lived to produce more offspring during the last several centuries.

The greatest documented predation on manatees today occurs incidentally in Florida due to competition for space between manatees and humans. Government agencies have been documenting manatee mortality in Florida for almost three decades. The proportion of deaths related to collisions with watercraft tends to increase each year as more and more people move to Florida. For current statistics on Florida manatee mortality, visit the FMRI and FFWCC websites at www.fmri.usf.edu/manatees.htm and www.state.fl.us/fwc/psm/manatee/manatee.htm. Even the most elusive manatee has a difficult time avoiding interaction with people as the human population and development continue to grow.

Osmoregulation: Unlike the Amazonian manatee, which is endemic to the fresh waters of the Amazon River basin, and the dugong, which is only found in marine habitats, the West Indian and West African manatees appear to move freely between fresh and marine environments. Although the Florida subspecies is usually associated with fresh or brackish water, it is occasionally found far offshore in high salinity water (Reynolds and Ferguson 1984). Large amounts of barnacle growth suggest that some **individual**s spend prolonged periods in marine environments (Husar 1977, Hartman 1979). Antillean manatees are found year round in totally marine environment of red mangrove islands in Belize (personal observation). How does this species osmoregulate as it moves among fresh, brackish, and saltwater? Two alternative hypotheses come to mind: (1) West Indian manatees have physiological adaptations that enable them to maintain water balance and/or (2) W. I. Manatees behaviorally maintain water balance by seeking out fresh water sources in marine environments. Graham Worthy, a physiologist at Texas A&M University, and his students are working on this and **proximate cause** questions involving physiology. Preliminary results indicate that W. I. Manatees are "good osmoregulators regardless of the environment" (Ortiz et al. 1998).

A FEW THOUGHTS…

As we examine problem-solving behavior in the West Indian manatee using the ethological perspectives of **cause**, **development**, **evolution**, and **function**, we begin to realize how many questions remain un-answered about this elusive marine mammal. Although we know (from the study of other mammals) that the **proximate cause** of behavior is a complex interaction between internal mechanisms and external stimuli, we don't know the specific triggers for many manatee behaviors.

Proximate development has not been well studied for several reasons. Free ranging female manatees with new calves tend to isolate themselves in secluded areas making behavior difficult to observe. Observations of captive raised manatees may not be indicative of normal development. The West Indian manatee is an endangered species making experimental manipulation difficult, yet extremely important to the successful rehabilitation and release of injured manatees. For example, how will a captive raised calf learn to find warm water effluents during cold spells? Can adult manatees learn successful migration routes or must they be learned during early development? From an **ultimate** perspective, manatees are also quite challenging due to the lack of closely related **extant** species and to the sparse fossil record. But, paleo-**sirenian** research, by Daryl Domning and others, continues to offer insight to the **evolution** and **function** of modern manatee behaviors. Why are there fewer **sirenian** species today than during the past? Does the **evolution** of the species Homo correlate with the decline of **sirenians** or were other environmental factors the reason for their **extinct**ions? Will answers to these and other **ultimate** questions aid in our conservation efforts?

Although manatees are generally considered elusive, there are cases where they appear to be curious and actually initiate contact with humans. Likewise, many behaviors tend vary between **individual**s, **population**s, and species. Because of the variable nature of manatee behavior, we must be careful in applying what we know about the Florida **population** to other areas. The Florida subspecies is fortunate to have the efforts of many US citizens and agencies working toward conservation issues and manatee behavior plays and important role in making management decisions in Florida. However, West Indian manatees are considered endangered throughout their range. Continued research effort on **population**s in the more tropical regions of the Caribbean is necessary for decision makers in those countries to make effective management decisions.

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Sea World Education Department: www.seaworld.org/manatee/manatees.html

Florida Power & Light Company: www.dep.state.fl.us/psm/webpages/manatees/booklet.html
University of Wisconsin - The Brain of the Florida Manatee: www.neurophys.wisc.edu/manatee/
University of Florida - Manatee Research Group: www.vetmed.ufl.edu/ufmrg/manatee/

GLOSSARY

agonistic: a general term that includes aggressive, submissive, and defensive behaviors that appear when the adrenal hormones are activated.
anecdote: a short story or observation which has not been "tested" by the scientific method.
anthropocentric: considering human beings as the most significant entity of the universe; interpreting or regarding the world in terms of human values and experiences.
anthropogenic: of, relating to, or resulting from the influence of human beings on nature.
anthropomorphic: described or thought of as having a human form or human attributes; ascribing human characteristics to nonhuman things.
bogue: the local term for a channel of water that flows through a mangrove caye in Belize, C.A.
cause: stimulus outside the animal plus the internal physiological state of the animal.
Cetacea: the order of aquatic mostly marine mammals that include the whales, dolphins, porpoises, and related forms and that have a torpedo-shaped nearly hairless body, paddle-shaped forelimbs but no hind limbs, one or two nares opening externally at the top of the head, and a horizontally flattened tail used for locomotion.
convergent: similar traits in species from very different genetic lineages, due to similar environmental **function**s.
development: changes in behavioral traits as an **individual** ages.
divergent: different traits in species from similar genetic lineages due to differences in their environments.
endemic: restricted or peculiar to a locality or region. Amazonian manatees are only found in the Amazon River Basin.
ephemeral: short period of existence; opposite of eternal.
estrous: the period during which a female has produced an egg ready to fertilize and is receptive to copulation.
evolution: change in proportion of genotypes within the gene pool of a **population** over many many generations.
extant: currently or actually existing; not destroyed or lost.
extinct: no longer existing.
extirpated: to destroy completely.
folk psychology: a non-scientific way of talking about animal behavior. Uses human terms to describe non-human animal behavior. Intuitive – based on anecdotes, experiences, observations. **Anthropomorphic**. Assumes that animals have beliefs, feelings, desires.
function: the meaning of a behavior in terms of survival and reproduction in a given environment.
gestation: the carrying of young in the uterus.
herbivores: animals that feed exclusively on plants.
individual: a single organism; a way of understanding the biological hierarchy of concepts - those pertaining to physiological processes and experiences of each organism; in contrast to **population**, which focuses more on gene pools of groups of animals that interbreed.
lactation: the secretion of milk.
manatee hole: concave depression in sandy or muddy substrate where manatees habitually rest.
mating herd: the name given an **estrous** female and the aggregation of males which follow her around attempting to mate.
mating system: males strategies and female strategies as observed in a **population**.
morphology: the form and structure of an organism or any of its parts.
natural selection: the process that produces **evolution**ary changes in a **population** due to heritable traits in some **individual**s which result in those **individual**s being more reproductively successful; the process only occurs IF (1) there are variances in traits within a **population**, (2) the variances are heritable, (3) **individual**s with certain variances have greater reproductive success than **individual**s with other variances, then over time, we would expect to see the trait selected "for" become more common in the **population**.
neonate: term used distinguish a newborn cetacean or sirenian calf from an older calf – you can still see the fetal folds on a neonate and the skin is usually darker than on an older calf.
osmoregulation: regulation of osmotic pressure especially in the body of a living organism. how an organism regulates the amount of water entering and leaving its body.
parturition: the action or process of giving birth to offspring; birth, whelping.
pinniped: any of a suborder (Pinnipedia) of aquatic carnivorous mammals (as a seal or walrus) with all four limbs modified into flippers.
polyandry: a **mating system** where one female mates with two or more males at a time. (adj: **polyandrous**)

population: a group of animals that interact and interbreed.
postpardum: following **parturition**; after giving birth.
prehensile: an appendage adapted for seizing or grasping especially by wrapping around - examples: a monkey has a **prehensile** tail and an elephant has a **prehensile** trunk.
proboscis: the trunk of an elephant; also any long flexible snout; any of various elongated processes of the oral region of an invertebrate.
promiscuity: a **mating system** where there is no prolonged association between the mating pair and at least one sex engages in multiple mates. (adj: **promiscuous**)
proximate: immediately preceding or following as in a chain of events, causes, or effects; in ethology - the perspective that looks at the **cause** and **development** of behavior at the **individual** animal level.
scramble-polygyny: a **mating system** where many males try to mate with many females, but without overt competition among themselves.
Sirenia: the taxonomic order of aquatic herbivorous mammals including the manatee, dugong, and Steller's sea cow. **Sirenians** are members of the Order Sirenia.
social animals: tending to form cooperative and interdependent relationships with others of one's kind; living and breeding in more or less organized communities.
taxonomy: orderly classification of plants and animals according to their presumed natural relationships; the study of the general principles of scientific classification; systematics.
thermoregulate: the maintenance or regulation of temperature; specifically the maintenance of a particular temperature of the living body.
ultimate: most remote in space or time; last in a progression or series; in ethology - the perspectives of **evolution** and **function** that look at behavior at the **population** and/or species level.
uniparous: producing one offspring at a time.

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