HABITAT USE PATTERNS AND RANGES OF THE BOTTLENOSE DOLPHIN IN THE GULF OF CALIFORNIA, MEXICO

LISA TAYLOR BALLANCE
Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, California 95039

ABSTRACT
I studied behavior and range patterns of individual bottlenose dolphins during 1984 in the mid-eastern Gulf of California, Mexico. Dolphin sighting rate was significantly higher in areas close to estuary mouths, 0.306 sightings per hour compared with 0.155 sightings per hour in areas distant from estuary mouths. Dolphins used these estuarine areas to feed; 61% of all behavior observed near estuaries was feeding as compared with 23% elsewhere. Traveling comprised 61% of all behavior observed in areas distant from estuary mouths. Estuaries are sites of large concentrations of nutrients which support great numbers of filter-feeding zooplankton and fish. Bottlenose dolphins may specialize on estuarine prey, or they may feed in estuarine areas simply because of the abundance of potential prey that these systems support. In either case, data on relative numbers, distribution patterns, behavior and diet indicate that this is a general trend in habitat use for many coastal populations of this species in the Pacific and Atlantic.

Ranges of a few individuals spanned a minimum of 65 km of coastline, and animals were not permanent residents of a monitored bay. In contrast, dolphins off the coast of Sarasota, Florida, have been reported to be year-round residents with smaller ranges. This difference in degree of site fidelity may be related to habitat differences. The west coast of Florida is dotted with numerous and large estuarine systems which may host permanent prey populations and support resident groups of dolphins. The Gulf of California coastline contains few estuaries; most are small and perhaps support prey resources which are ephemeral, requiring dolphins to range over larger distances in search of food.

Key words: bottlenose dolphin, *Tursiops truncatus*, behavior, habitat use, home range, photo-identification.

Habitats are generally composed of a mosaic of patches which differ from each other physically and biologically. Some patches offer more protection from the elements or from predation; others offer less. Some patches support large concentrations of food; others are barren. Because of such heterogeneity we
expect to see specific patterns in the way animals are distributed and in the way they use patches within a given habitat.

This is the case for several species of cetaceans. Spinner dolphins (*Stenella longirostris*) in the Hawaiian islands rest in shallow, sandy areas in coves or atolls during the day and move into deep water to forage at night (Norris and Dohl 1980). Humpback dolphins (*Sousa* sp.) along the southeastern coast of South Africa feed among reefs along an unsheltered, rocky coastline, but rest, mate, play, and move within a sheltered bay with a sandy bottom (Saayman *et al.* 1972, Saayman and Tayler 1979). Killer whales (*Orcinus orca*) in Puget Sound feed over areas of high relief in bottom topography and travel across deep water areas with relatively little topographic relief (Heimlich-Boran 1987).

Habitat heterogeneity and the biological requirements of a species interact not only to produce these patterns in distribution and in habitat use, but also to influence the size of an animal’s home range (McNab 1963). Specifically, the body size and energy requirements of an animal dictate the amount of energy necessary to maintain this individual. The abundance, distribution and availability of resources within the habitat determines the size of an area which will fulfill these energy requirements. The result of the interactions between these factors is manifested in the size of the home range.

These factors, distribution, habitat use patterns and home range size, are intricately related to features of an animal’s habitat. In this paper, I document distribution, habitat use patterns, and range of bottlenose dolphins (*Tursiops truncatus*) in the Gulf of California, Mexico. I then compare these characteristics to a population of bottlenose dolphins off the west coast of Florida and conclude that specific habitat features may influence ranging behavior of this species.

**METHODS**

Research was conducted during the spring, summer, and fall of 1984, along the west coast of mainland Mexico in the Gulf of California (Fig. 1). I surveyed 200 km of coastline and waters around mid-gulf islands at a constant speed of five knots from one of two boats: a 3.6-m, 165-hp inboard-outboard Stemcraft or a 10-m, twin 155-hp Skipjack during 562.2 h. Of these, 186 h were spent in direct observation of bottlenose dolphins. Prior to this, a pilot study was conducted during the summer of 1983. None of the 1983 preliminary data are included in the present analyses.

Once a group was sighted, I followed and observed dolphins from a distance of 50 m or more for periods of 30 min to 6 h. During this time, I continuously recorded location, movements, and number of individuals in the group. I monitored weather, sea conditions, water depth, water temperature, and secchi disc depths each 15 min.

I also monitored activity patterns. Groups habituated to the boat and resumed their normal activity within half an hour after observations began. Accordingly, I continuously recorded the behavioral state of dolphins from 30 min after the initial sighting of the group until the end of the observation period for that group. All individuals in a group exhibited the same general behavioral state;
Figure 1. Map of the study area, the mid-eastern Gulf of California, and sighting locations of dolphin groups, indicated by shaded areas. The number of individuals resighted in each area and location of animals sighted in more than one area are indicated. The inset gives location and date of sightings of animals photographed in more than one area.

The behavior patterns I recorded represented the activity of each group as a unit. I classified activity into one of several categories which are described below. I did not quantify discrete behaviors such as leaps, spy hops, tail slaps and vocalizations.

The dorsal fins of *Tursiops* are regularly nicked and scarred, and these markings are unique features which can be used to identify individuals (Wiirsig and Wiirsig 1977, Ballance 1990). In order to monitor the movements and associations of individual animals, I attempted to photograph the dorsal fin of each animal in all groups. I used an Olympus camera with a motor drive and data back, a 200-mm lens and Kodachrome (K-64) color slide film. I took over 7,000 photographs during the study. In the laboratory, I identified individuals from these photographs by viewing the slides under a dissecting microscope.

The 200 km of coastline I surveyed included a variety of habitats ranging from shallow, turbid waters with sandy bottoms to rocky shores dropping abruptly to deep depths in clear water. I assessed the distribution and behavior patterns of *Tursiops* for two habitat types: estuarine and non-estuarine. I arbitrarily chose three nautical miles (5.5 km) to define the boundary between these two habitat types: waters within three nautical miles of the mouth of an estuary...
were labeled estuarine and waters farther than three nautical miles were labeled non-estuarine. Habitat use was compared by calculating the number of sightings of dolphin groups in a particular habitat divided by the number of hours spent surveying this habitat.

I quantified ranges by analyzing photographs of individuals from the entire study area and calculating distances between areas in which the same animal was sighted. I use the term “range” simply to denote that area within which an animal has been sighted. This is distinct from “home range” which is defined as the area over which an animal normally travels in pursuit of its routine activities (Burt 1943). Conclusions about an animal’s home range may be made only after details about daily and seasonal movements and activities are known. Results of this study comprise a series of sightings of individual animals; these sightings outline only a portion of the home range of these individuals.

RESULTS

Behavior—Behavior of bottlenose dolphins could readily be classified into four categories which I have termed feeding, traveling, resting, and socializing.

Feeding was characterized by no directional movement. Animals generally surfaced and dove asynchronously while the entire group remained loosely aggregated over an area of several hectares. Occasionally, an individual would pursue prey at the surface by swimming upside down at high speed with pectoral fins in the air. These animals were apparently feeding individually. On a few occasions, animals appeared to feed cooperatively, surfacing synchronously in a large circle, then diving in toward the center. Tightly grouped balls of bait fish were sometimes visible beneath the surface in the center of the area where the dolphins dove. I directly witnessed prey capture by dolphins on a few occasions, when dolphins were exhibiting each of the above behaviors.

Seabirds were frequently present with feeding groups of dolphins. Brown pelicans (Pelecanus occidentalis), blue-footed and brown boobies (Sula neubouxi and leucogaster), double-crested cormorants (Phalacrocorax auritus), and magnificent frigatebirds (Fregata magnificens) were the most common species associated with these feeding groups. Flocks of these seabirds, circling and diving, were so indicative of feeding dolphins that this became one of the most reliable methods of locating a group and classifying feeding behavior.

Traveling was characterized by directional movement of a group. Traveling animals moved as a unit, diving and surfacing synchronously at speeds of three to five knots. Dives averaged two and one-half to three minutes and surface intervals consisted of several respirations during a time interval of approximately 30 sec.

Resting was characterized by low levels of activity during which almost no forward movement of animals occurred. A resting animal slowly rose to the surface with its head and dorsal fin breaking the water simultaneously, remained afloat for up to 10 sec, and slowly submerged again with almost no forward rolling motion.
Socializing was characterized by a high level of activity. Socializing animals surfaced together in a tight aggregation and often remained at the surface for several minutes. During this time, animals exhibited prolonged body contact and furious activity. Body contact often took the form of slaps of the flukes or pectoral fins of one animal against the body of a second.

Traveling and feeding occasionally occurred simultaneously with animals moving along a coastline, stopping to feed, and resuming travel once more. Traveling also occurred in conjunction with socializing. No other combination of two or more behaviors was observed.

**Habitat use patterns**—I observed 93 groups of bottlenose dolphins during the study. These groups were not dispersed evenly over the entire study area. Dolphins were generally sighted in shallow, turbid water where the bottom was composed of sand. Dolphins also remained close to the coast. Only three groups moved farther than five km from shore, and the majority were observed within three km from shore. Water near rocky coastlines, water over 10 m deep and clear water were areas of few dolphin sightings.

Dolphin sighting rate and number of schools were highest in areas near the mouths of estuaries (Table 1). Twice as many groups per hour were sighted in areas within 5.5 km from the nearest estuary mouth as compared with areas farther than 5.5 km from the nearest estuary mouth. This difference in sightings per hour was significant ($\chi^2 = 8.33; P < 0.05$).

Dolphins used these habitats near estuary mouths to feed (Fig. 2). Sixty-one percent of all behavior observed in areas within 5.5 km of an estuary mouth was feeding. The next most prevalent behavior was traveling, comprising 22% of the behavior in these areas. In areas farther than 5.5 km from an estuary mouth behavior was strikingly different. Sixty-one percent of all behavior observed here was traveling; 23% was feeding. Resting and socializing comprised approximately the same percentage of the behaviors observed in both locations.

**Ranges**—Ninety-three dolphin groups were sighted in eight separate locations (Table 2). The vast majority of these were sighted in Bahia Kino, as expected from the high number of survey days in this area. The number of groups sighted in the seven areas outside of Kino is low because of the small number of survey days in these areas.

Two hundred six individual dolphins were identified during the study. Of these, 155 were sighted in Bahia Kino and 51 were sighted in seven additional locations along the coast to the north and south of Bahia Kino and around several offshore islands (Fig. 1 and Table 2).

The 155 individuals identified in Bahia Kino represented a majority of the animals visiting this bay during the study period (Ballance 1990). Seventy-five individuals were identified during the first month of the study, from mid-May to mid-June. Another 75 were identified during the last three weeks of October. But during the months of November and December, only five previously unidentified individuals were photographed in Bahia Kino. This means that these animals could be recognized if they traveled to other locations within the study area.

Many individuals were sighted in the same location more than once (Fig. 1).
Figure 2. Behavior of bottlenose dolphins in two habitat types: areas near and far from estuaries. Light-colored bars indicate behaviors observed in waters farther than 5.5 km from an estuary mouth; dark-colored bars indicate behaviors observed in water closer than 5.5 km from an estuary mouth. Letter abbreviations represent behavior categories: F = feeding, T = traveling, R = resting, S = socializing. Numbers above each column represent hours of observation of each behavior category.

Ninety-four of the 155 individuals identified in Bahia Kino were sighted there between two and 11 times (Ballance 1990). Three of the seven animals identified in Guaymas were sighted there twice: two animals on 7 and 8 July and one animal on 11 and 12 November. One of the 16 animals identified in Estero Tastiota was sighted there twice, on 24 and 25 July. Two of the 12 dolphins identified in Bahia Agua Dulce were seen there twice, both animals on 17 and 18 July. All of the animals resighted in the areas outside of Bahia Kino and many of those resighted in Bahia Kino were sighted on adjacent days.

Of the 206 individuals identified throughout the study area, only five were seen at more than one location (Fig. 1). The distance between sightings for these individuals varied from 25 to 65 km.

**Discussion**

It is widely believed that a single species of bottlenose dolphin is cosmopolitan and exhibits a series of forms which differ behaviorally and morphologically (Leatherwood and Reeves 1983a). Results of this study pertain only to the inshore, coastal form, although both inshore and offshore morphs have been reported in the Gulf of California (Walker 1981).

**Behavior**—Bottlenose dolphin behavior is generally described in terms of four major categories: feeding, traveling, social interactions, and idling (Shane et al.
Table 1. Bottlenose dolphin presence in two habitat types, areas near and far from estuaries. Group sighting rate was significantly higher in areas close to an estuary mouth.

<table>
<thead>
<tr>
<th>Distance to estuary mouth</th>
<th>Survey effort (hours)</th>
<th>Dolphin groups sighted</th>
<th>Sightings per hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;5.5 km</td>
<td>228.5</td>
<td>70</td>
<td>0.306</td>
</tr>
<tr>
<td>&gt;5.5 km</td>
<td>148.0</td>
<td>23</td>
<td>0.155</td>
</tr>
</tbody>
</table>

1986), and the dolphins in this study exhibited behavioral patterns which clearly fell into these four groups.

Feeding is a particularly interesting behavior because of the diversity of specific techniques that have been documented for this single species (reviews by Leatherwood 1975, Shane et al. 1986, Shane 1990b). In Bahia Kino feeding individually, presumably on dispersed prey items, was the predominant strategy. I also observed a few instances of apparent cooperation between the individuals of a group.

Shrimp boats operated in the area during approximately one-half of the study and were often trawling or hauling in nets within a few km of a dolphin group. In the Gulf of Mexico dolphins frequently feed behind working shrimp boats during all stages of the fishing operation (Gunter 1942, Caldwell and Caldwell 1972, Leatherwood 1975, Gruber 1981, Goodwin 1985). I never observed Gulf of California dolphins feeding behind these working shrimp trawlers.

Habitat use patterns—Bottlenose dolphins in the Gulf of California were sighted most often in areas close to estuaries, and the animals used these areas to feed. The use of estuarine areas as feeding sites may represent a trend in habitat use by many coastal populations of bottlenose dolphins.

Estuarine areas repeatedly have been found to be sites of high dolphin occurrence. Along the U.S. coast of the Gulf of Mexico preferred areas include ship channels, passes between inshore bays and the open ocean, river mouths, bays, lagoons, and estuarine complexes (Gunter 1942; Barham et al. 1980;...

In addition, behavioral observations indicate that bottlenose dolphins feed in estuarine areas. Many studies report details of feeding behavior from observations made in estuarine systems (Hoese 1971; Shane 1977, 1987; Leatherwood 1975, 1979; Gruber 1981; Irvine et al. 1981; Goodwin 1985). Shane (1990a) found that bottlenose dolphins off the west coast of Florida spent more time feeding in bay areas with seagrasses and mangroves than in surrounding Gulf waters.

Estuaries characteristically contain high concentrations of nutrients, zooplankton and fish (Moyle and Cech 1982). Presumably, it is these large concentrations of potential prey which attract dolphins to these habitats. There are two types of estuaries. The most common is a semi-enclosed coastal body of water having a free connection with the open ocean and brackish water within, resulting from a dilution of sea water with freshwater deriving from land drainage (Cameron and Pritchard 1963). Most of the embayments on the east, west and Gulf of Mexico coasts of the United States fall within this definition. A second type of estuary, often termed a negative estuary and more typical of those in the Gulf of California, receives little freshwater runoff over the course of a year, and consequently, the water in these embayments becomes progressively more saline further inland (Nybakkken 1982). Despite these physical differences, both types of estuaries are sites of large concentrations of nutrients which, in turn, support great numbers of filter-feeding zooplankton and fish (Vannucci 1969, Thomson 1973).

Coastal bottlenose dolphins may specialize on estuarine species (Barros and Odell 1990). In support of this is the fact that a large proportion of the species reported as prey items are found in estuaries (Ballance 1987, Shane 1990b). However, bottlenose dolphins are generalists. They are found in a wide range of habitats; they prey on a large number of fishes and invertebrates; they have demonstrated the use of multiple techniques for prey capture (Gunter 1942, Caldwell and Caldwell 1972, Leatherwood 1975, Leatherwood and Reeves 1982, Shane et al. 1986, Barros and Odell 1990, Cockcroft and Ross 1990, Mead and Potter 1990, Shane 1990b). Rather than specializing on estuarine species, it is quite possible that dolphins feed in estuarine systems simply because of the high abundance of potential prey that such systems support.

Obviously, diet preferences and seasonal variations should be studied in much greater detail before estuaries can be identified as primary feeding areas for bottlenose dolphins. But estuaries are, doubtless, sites of high concentrations of fishes and invertebrates. Behavioral evidence strongly indicates that areas near estuary mouths are preferred feeding sites for Gulf of California bottlenose dolphins. And data on numbers, distribution patterns, behavior and diet indicate that this is a general trend in habitat use for many coastal populations of this species.

Range—The bottlenose dolphins identified in Bahia Kino were not residents
of this bay and therefore, ranged outside of this area (Ballance 1990). Thirty-nine percent of all dolphins identified in Bahia Kino were sighted there only one time. Of those individuals sighted more than once, the average time span between adjacent sightings was 30 d. And there was a notable seasonal flux of dolphins into and out of Bahia Kino.

The size of the range of several photographically identified individuals spanned a minimum of tens of kilometers of coastline. Dolphins A and B were sighted in locations separated by 25 km, dolphin #43 in locations separated by 60 km, and dolphins #29 and #112 in locations separated by 65 km.

A very small proportion of the individuals sighted in Bahia Kino also were sighted at other locations: three animals from a total of 155 identified individuals. These animals were not constant residents of Kino (Ballance 1990) and so, must have been using additional areas. Yet, they were not seen in those areas surveyed along 200 km of coastline. It is likely that with more survey effort in adjacent areas, more of the dolphins identified in Kino would have been resighted. However, one-quarter of the individuals identified in this study were sighted in these adjacent areas, and these were not dolphins that had been seen in Bahia Kino. Therefore, it seems likely that many of the animals sighted in Kino may have been ranging outside of the study area.

Several other studies indicate that ranges of coastal bottlenose dolphins can be large. Defran et al. (1985) reported sightings of San Diego bottlenose dolphins off the coast of Baja California. Gruber (1981) identified an animal off the coast of Texas that had previously been sighted 95 km to the southwest. Hansen (1983) resighted 12 dolphins first identified off the coast of San Diego, in locations ranging from 140 to 185 km to the north. Würsig and Würsig (1979) sighted individuals from their study population at Golfo San Jose, Argentina, 300 km away from the study area. Wolf et al. (1987) reported sightings of one dolphin in waters off Santa Barbara, California, and 483 km to the south off the coast of Ensenada. And Wells et al. (1990) reported a 1,340 km round trip for San Diego dolphins sighted in Monterey Bay.

The most detailed work on ranges of bottlenose dolphins has been conducted near Sarasota, Florida (Irvine and Wells 1972; Wells 1978, 1986; Wells et al. 1980; Irvine et al. 1981; Scott et al. 1990). Here, a population of approximately 100 individuals are residents of a home range area of approximately 85 km². Animals are year-round residents; immigration and emigration are rare. Animals are found in groups segregated according to age and sex, and these different segments of the population use different parts of the home range preferentially with the result that female-calf pairs, subadults and adults, males and females have varying home range sizes and locations.

Results from the present study pertain only to ranges of Gulf of California bottlenose dolphins, not to home ranges as in the Sarasota study. Still, some basic comparisons between residence patterns and ranging behavior reveal an interesting difference in site fidelity. While the dolphins in the Sarasota Bay area were residents of this region and rarely visited adjacent waters, dolphins in the mid-Gulf of California appeared to range more freely. Many dolphins visited Bahia Kino but were not continuously present in this bay (Ballance 1990).
This difference in site fidelity may be related to habitat differences (Ballance 1990). The west coast of Florida is lined with barrier islands which form numerous, large shallow bays and channels. The Gulf of California is an open coastline with few protected bays and inlets. Perhaps the large estuarine systems of the west coast of Florida support permanent prey resources and allow for resident populations of dolphins, while the smaller estuaries of the Gulf of California provide only temporary, more ephemeral prey resources, prompting dolphins to range between these areas in search of food. Additional study of residence patterns of bottlenose dolphins in differing habitat types would provide evidence to further address this possibility.

ACKNOWLEDGMENTS

I would like to express my deepest gratitude to Harry and Vilma Ballance. Their support in all aspects of this study, from field assistance, to financial support, to intellectual stimulation, was invaluable. Without their help, this research would not have been possible. I am indebted to Don Croll for field assistance, technical and analytical expertise, and intellectual support. Bernd Würsig gave me field assistance, advice and friendship, and was an invaluable teacher.

My sincere thanks also go to Bernie Tershey and Craig Strong for dorsal fin photographs, Lloyd Findley and Omar Vidal for support and assistance with permits, Greg Cailliet, Robert Pitman, Michael Scott, Randy Wells and Bernd Würsig for insightful comments on earlier versions of the manuscript, Steven Young for help in final manuscript preparation, Robert Holland, Don Thompson and the Department of Ecology and Evolutionary Biology at the University of Arizona for figure preparation, and the members of the Club Deportivo, especially Eldon and Joanie Heaston, Bob and Frankie Jarrett, and Roy and Mary Francis Morwood, and to Gregorio Camacho Molina, who offered me their friendship, interest, knowledge, and constant logistical and emotional support.

I received funding from the American Museum of Natural History, The Packard Foundation, and The American Cetacean Society. I am indebted to the Secretary of Fisheries of Mexico for allowing me to work in the Gulf of California under permit number 3717.

LITERATURE CITED


Leatherwood, S. 1975. Some observations of feeding behavior of bottlenosed dolphins (Tursiops truncatus) in the northern Gulf of Mexico and (Tursiops cf. T. gilli) off southern California, Baja California, and Nayarit Mexico. Marine Fisheries Review 37:10–16.


Received: May 13, 1991
Accepted: November 4, 1991