

Organization and social structure of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf de Guayaquil, Ecuador

Fernando Félix

Fundación Ecuatoriana para el Estudio de Mamíferos Marinos (FEMM), PO Box 09-01-11905 Guayaquil, Ecuador

Abstract

A study on the coastal bottlenose dolphin was carried out between February 1990 and October 1992 in the inner estuary of the Gulf of Guayaquil, Ecuador (3°S, 80°W). In 143 boat surveys, a total of 4021–4351 dolphins in 241 groups were recorded. 441 different dolphins were identified by natural marks of which 1557 resightings were obtained. Based on resightings, it was established that this population of dolphins is organized in communities of around 115 animals (S.D.=37). Three resident and two non-resident communities were recorded in the study area. Resident communities occurred along 20–40 km of coast in overlapping home ranges. There were interactions between groups of different communities in 13.3% of the observations. Association patterns among individuals of different age and sex classes were analyzed. Females mainly associated with other females and formed bands. Every band showed preferences to use different sites of the community home range. Subadults associated to a particular adult female band. In contrast, adult males did not show preference to associate with any band. Several males occurred in high-stable pairs and competed for females in what seems to be a hierarchically structured society, with one pair of dominant males controlling the access to females in the community. These findings suggest a marked polygynous mating behavior in this tropical population that contrasts to what was observed in other temperate and subtropical populations.

Introduction

Like many terrestrial mammals, dolphins have a complex social organization. Studies on wild odontocetes have been carried out mainly on coastal populations such as humpback dolphin *Sousa* sp. (Saayman & Tayler, 1979), killer whales *Orcinus orca* (Bigg, 1982; Bigg *et al.*, 1990) and especially the bottlenose dolphin *Tursiops truncatus* (Tayler & Saayman, 1972; Würsig, 1978; Wells *et al.*, 1980; Irvine *et al.*, 1981; Wells *et al.*, 1987;

Ballance, 1990), although some oceanic species such as spinner dolphin *Stenella longirostris* (Norris & Dohl, 1980) and short-finned pilot whale *Globicephala macrorhynchus* (Heimlich-Boran & Heimlich-Boran, 1990) have also been studied near islands. Most of these societies are characterized by having an open structure with groups interchanging members continuously and, in the case of coastal species, possess well-defined home ranges. However, different species and even different populations of the same species show variety in their social organization in response to environmental conditions like availability and distribution of food resources, density of predators and physical characteristics of the habitat (Wells *et al.*, 1980).

Because dolphins are long-lived animals it has been demonstrated that long-term studies are necessary in order to know more subtle aspects of their social structure (e.g. Bigg *et al.*, 1990; Scott *et al.*, 1990; Wells, 1991). In the particular case of the bottlenose dolphin, a more complete approach has been obtained thanks to the exhaustive studies carried out in Sarasota Bay, Florida, where capture-release operations have occurred during selected years over the last twenty-five years (Wells *et al.*, 1980; Irvine *et al.*, 1981; Wells *et al.*, 1987; Scott *et al.*, 1990; Duffield & Wells, 1991; Wells, 1991).

A long-term study of a resident bottlenose dolphin population in the inner estuary of the Gulf of Guayaquil, Ecuador (Fig. 1) began during 1990. Their movements, distribution, feeding habits and other ecological aspects are now better known (Félix, 1994). In this paper their organization and social structure are described, including group composition, home ranges and individual association patterns. Also, the effect of a tropical environment on reproductive behavior and social structure is compared with more studied temperate and subtropical populations.

Study area

The Gulf of Guayaquil is the largest estuary on the Pacific coast of South America (Fig. 1). Located 3°

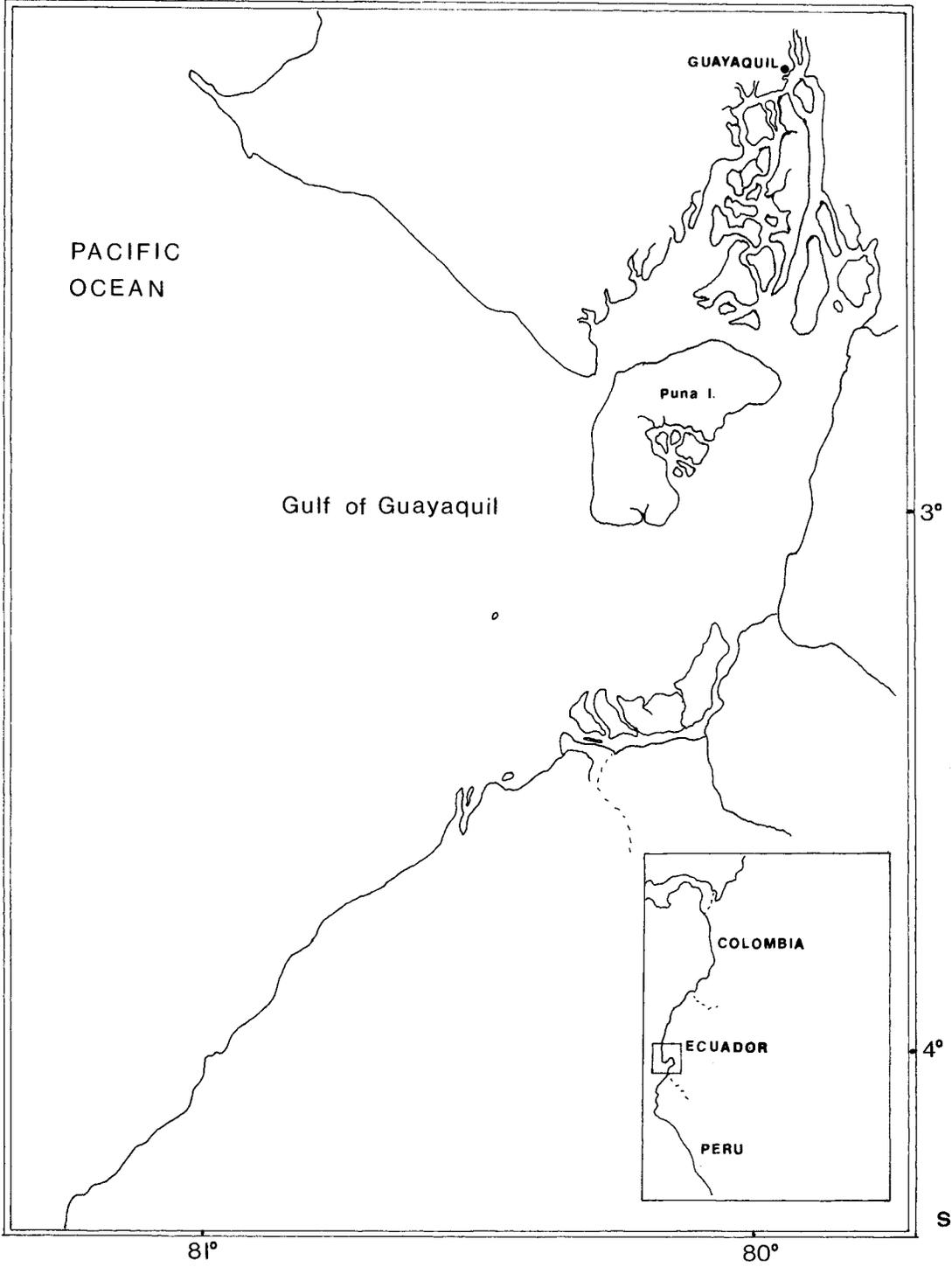


Figure 1. The Gulf of Guayaquil.

south of the equator, the entrance of the Gulf is 204 km wide and extends inland for 130 km. The Gulf is naturally divided into an outer estuary that starts near the western side of the Puná island (80°15'W) and ends along 81°W longitude, and an inner estuary that extends northeast from Puná Island for 74 km before narrowing into the main course of the Guayas River, the main contributor of freshwater runoff into the estuary (Stevenson, 1981). Another channel, west and parallel to the Guayas River (the Estero Salado) extends up to the city of Guayaquil. Between the Estero Salado and Guayas River are several narrow channels and islands, completely or partially covered with mangrove.

The inner estuary has a strong tidal current of up to 4 knots (Stevenson, 1981). The tidal range oscillates between 2.6–3.5 m. Almost the whole inner estuary has a depth of less than 10 m. (INOCAR, navigation chart I.O.A. 107).

Methodology

From February 1990 until October 1992, boat surveys ($n=143$) were carried out through the inner estuary of the Gulf of Guayaquil in a 4.8-m long fiberglass boat with a 75-HP outboard motor at 35–40 km/h. The surveys started in Guayaquil and ended at Río Hondo in Puná Island (Fig. 2). The return trip was made one or two days later. The main route went along the Guayas river and the east side of Puná island, but several alternate routes were taken as well, including the area of the north-western (the Estero Salado) and northeastern (the Mondragón Channel) parts of the inner estuary (see Félix, 1994, for survey details). Navigating time accounted for 1.112 hours spent at sea, including 260 hours of direct observations on the animals. A total of 4021–4351 dolphins was recorded in 241 different groups. During the trips the dolphins' dorsal fins were photographed for individual identification (see Würsig & Würsig, 1977); 441 different individuals were recorded of which 1557 resightings were made. Only natural marks were used for this purpose.

The position of each group was determined and each member was classified according to their relative size as follows: (1) adults, bigger and robust animals, generally with very distinctive nicks in the dorsal fins and in most cases accompanied by a calf; (2) subadults, less-robust and smaller animals, usually with less-distinctive nicks, or without nicks in their dorsal fins and not obviously associated with an adult, and (3) calves, smaller animals in close association with an adult and usually without nicks in their dorsal fins. According to their composition, the groups were divided into six types: all adults, all subadults, adults with subadults, adults with calves;

adults with subadults and calves, and unidentified (Table 2). The females were sexed when they maintained a close and durable relationship with a calf and were presumed to be mothers. The males were identified by photographs of their genital area when they leaped.

Naturally marked animals were used to estimate the size of the dolphin communities. For this purpose the Petersen estimator modified by Bailey (Seber, 1982, p.61) was employed, taking the number of different animals recorded in 1990 as the first sample and the animals recorded in 1991 as the second.

The association level between pairs of individuals, referred to as association coefficient (AC), was determined using the half-weight index (Cairns & Schwager, 1987) which is defined by the equation $2X/(Na+Nb)$, where X is the number of times that individual A and B were seen together and Na and Nb are the total number of sightings of each individual. The result obtained with this formula was multiplied by 100 to get a number between 0 and 100. Zero indicates that the pair was never seen forming part of the same group and 100 that the animals always were present in the same group. The association coefficients (AC) actually are underestimates because in most of the cases it was not possible to identify all the individuals present in the group. In order to avoid a larger bias, only those observations in which at least 50% of the individuals were identified were included in the analysis. Also, only those individuals that were sighted at least 5 times were considered. A one-way ANOVA test was used to determine if a significant difference existed among ACs of different age and sex classes.

The dolphins that inhabit the inner estuary of the Gulf of Guayaquil is considered to be a population in this article, although it is not likely a reproductively-closed unit. In 1991 it was estimated to be around 2500 animals (Félix, 1994). The population contains several communities made up of dolphins which regularly interacted with each other in greater degree than with dolphins from nearby areas (Wells *et al.*, 1987). A group was defined as dolphins that moved more or less in the same direction, or appeared to maintain contact, even when they were dispersed. Some individuals kept a closer contact with each other than with other members; these animals are referred to as a subgroup.

Results

Home range

Based on resightings of naturally marked animals it was determined that the population of bottlenose dolphin in the Gulf of Guayaquil is organized in small communities (Fig. 2). Within the study area,

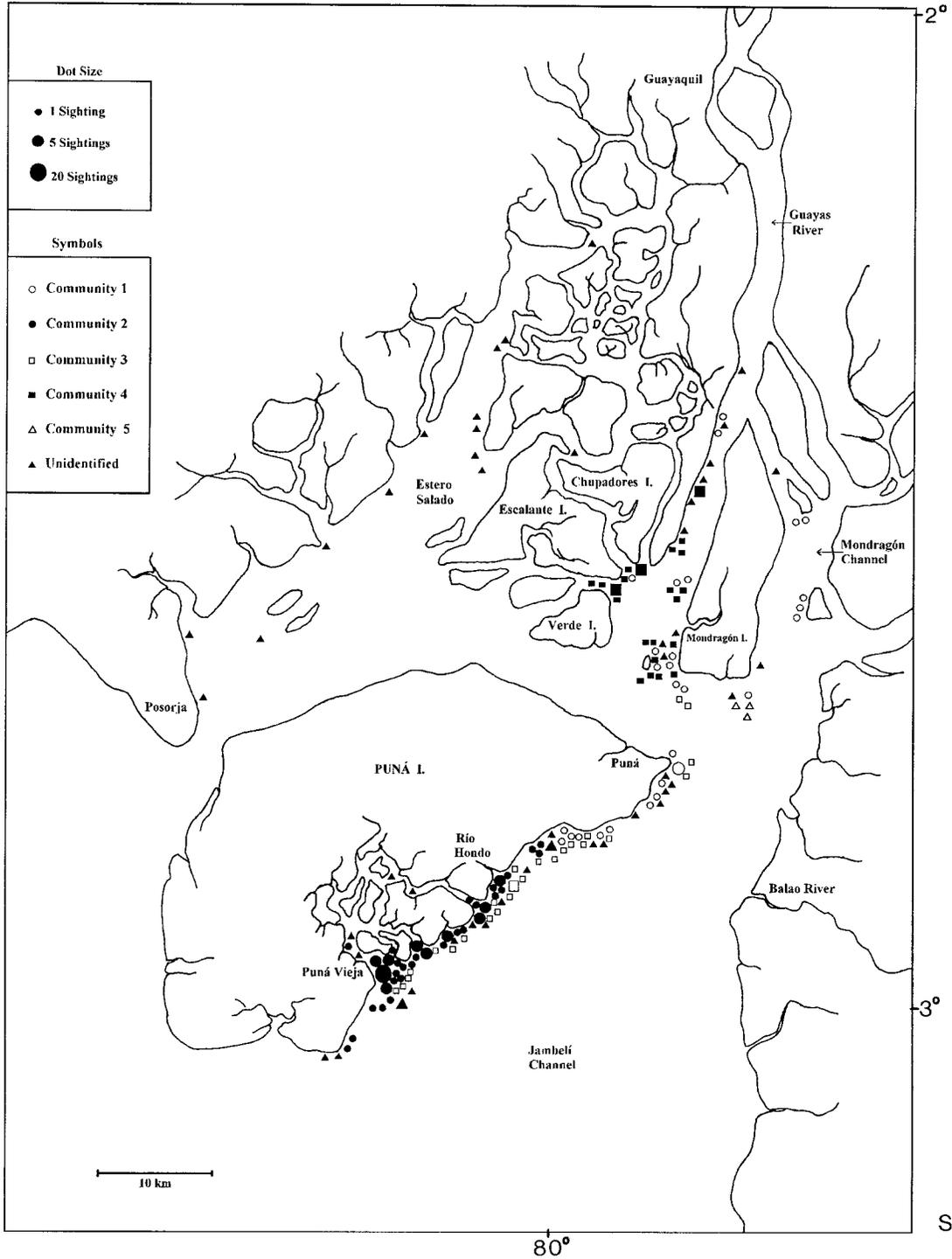


Figure 2. Sighting sites. The dots show the places where the groups were recorded in the study area. Every community is identified with a different symbol.

Table 1. Size of the bottlenose dolphin communities in the study area

| Item | Communities | | | |
|---|-------------|---------|---------|--------|
| | 1 | 2 | 3 | 4 |
| (A) Different dolphins sighted in 1990 (February 1990–January 1991) | 25 | 76 | 85 | 22 |
| (B) Different dolphins sighted in 1991 (February 1991–January 1992) | 37 | 79 | 91 | 70 |
| (C) Dolphins sighted both years | 16 | 49 | 48 | 12 |
| (D) Estimated abundance | 56 | 122 | 160 | 120 |
| C.I. 95% confidence interval | 36–75 | 102–142 | 130–190 | 63–177 |

covering 715 km² of the inner estuary of the Gulf of Guayaquil, five overlapping communities were identified and numbered from 1 to 5. Each community had its own home range, although the borders could not be defined clearly in every case. Some areas were frequented by individuals or groups from different communities or just used as transit zones.

Community home ranges differed in both size and physical characteristics. Some have parts with fresh and muddy waters, while others are located in more open, clearer water with a higher salinity. Communities #1 and #4 inhabited the northern part of the inner estuary and they both shared the outlet of the Guayas River, where the waters were brackish and turbid. Community #1 occupied the eastern riverside, the northeast part of Puná Island and all the northeastern part of the inner estuary (Mondragón Channel) for some 40 km. Community #4 occupied the west riverside and center of the Guayas River, the channels of the islands between the Guayas River and the Estero Salado and possibly the west side of the Estero Salado along at least 30 km. Groups of these two communities were sighted all year round. However, during the rainy season there was a significant decrease in the number of sightings in the outlet of the Guayas River (Félix, 1994), indicating a seasonal use of this part of their home range.

Community #2 inhabited the eastern and south-eastern part of the Puná Island, a 30-km stretch of clear and more saline water. Groups of this community were observed with the same frequency during all the year.

Two other communities, #3 and #5, were recorded seasonally and were regarded as transients to the area. Groups belonging to community #3 were sighted between May and October in 1990 and between May and December in 1991. In 1992, they were observed as early as March, but were more abundant from June onward. The range of this community included the outlet of the Guayas River to the southwestern tip of Puná Island (45 km

length) but it is unknown up to where they range the rest of the year. Less information was obtained about community #5; only three sightings of groups containing 60–80 individuals were made between May and August 1991 south to the Mondragón Channel. The groups formed by this community were the biggest observed.

Size of the communities

The communities contained between 56 and 160 dolphins ($X=115$, $S.D.=37$) (Table 1). Community #5 was not included in the table because in 1990 no dolphins belonging to this group were observed. More information was obtained from communities #2 and #3 and the estimated number could be considered more reliable than the other communities. In communities #1 and #4, an increase of 48% and 318% respectively in the number dolphins was observed in the second year. In the case of community #4, that increase could have been because groups of this community were sighted more often in 1991 occupying the outlet of the Guayas River, where the main survey route passes, than in 1990. In contrast to this, groups from community #1 were sighted with similar frequency in the area during both years. The biggest groups of this last community were observed in the Mondragón channel, which is in the northwest part of the inner estuary and out of the main route. Then, it is possible that the lower estimation obtained in this case was caused by a sampling artifact and not necessarily because the community was smaller.

Group composition

Group composition was similar in all the communities (Table 2). Most of the observed groups (64%) contained all the three age classes (adults, subadult and calves), followed by groups that consisted only of adults, adults with calves, adults with subadults, all subadults and unidentified. Groups containing all three classes were also the largest (25.4 inds./group, $S.D.=15.3$), while groups composed of all subadults and all adults were the smallest with an

Table 2. Age-class composition of the groups in each community and average group size

| Category | Communities (n) | | | | | | Total | | Average group size Inds./group |
|------------------------------|-----------------|----|----|----|---|-----|-------|------|-----------------------------------|
| | 1 | 2 | 3 | 4 | 5 | NIC | n | % | |
| Adults | 10 | 6 | | 2 | | 7 | 25 | 10.4 | 2.6 (S.D.=1.6) |
| Subadults | | 1 | | | | 11 | 12 | 5.0 | 2.3 (S.D.=1.3) |
| Adults and subadults | 6 | 4 | 1 | 3 | | 4 | 18 | 7.5 | 5.5 (S.D.=2.8) |
| Adults and calves | | 6 | 1 | 6 | | 7 | 20 | 8.3 | 5.9 (S.D.=4.7) |
| Adults, subadults and calves | 15 | 75 | 24 | 23 | 3 | 15 | 155 | 64.3 | 25.4 (S.D.=15.3) |
| Unidentified | | | 1 | | | 10 | 11 | 4.6 | 5.4 (S.D.=4.5) |
| | | | | | | | 241 | 100 | |

NIC=Non-identified communities.

average of 2.29 (S.D.=1.26) and 2.62 (S.D.=1.56) inds./group respectively. Of all observed animals, adults represented 51%, subadults 26% and calves 23%.

Interaction between individuals of different communities

On several occasions, dolphins from different communities, formed mixed groups. On 32 occasions (13.3% of the total groups sighted) groups with 1 or more individuals from two different communities were recorded, and on 2 occasions (0.8%) there were animals from 3 different communities. In most cases, the sexes of the involved animals were unknown, but in 3 cases females with calves were recognized. When 1 or 2 individuals from another community were present in a mixed group, they seemed to be integrated with other group members, but when greater numbers of animals were present, they generally formed a subgroup and maintained some autonomy.

Activities such as feeding and mating seemed to promote mixed groups. Feeding was observed in 41% of the mixed-group sightings ($n=13$) and mating involving individuals from different communities was observed on 6% ($n=2$). Mixed-group associations usually lasted only a few hours, but on two occasions the associations were more extended. In one of these, two adult dolphins from community #3 were sighted on two consecutive days with groups of community #2 whose composition was similar during both days. On another occasion a mother-calf pair from community #5 stayed at least two weeks with groups of community #3.

Patterns of individual association

Most of the information on association among individuals was obtained from dolphins of community #2 ($n=91$, 38% of the total groups observed). From 61 selected observations (those with at least

50% of the animals identified) a matrix of association with 49 individuals sighted at least 5 times was created (Fig. 3). These animals included 23 adult females, 11 subadults (three females and the remainder of undetermined sex), 3 adult males, 1 calf and 11 adults of undetermined sex. The average association coefficient (AC) among these animals was 32 (S.D.=18).

Associations among adult females

The ACs between pairs of adult females showed a wide range from 0 to 83. Because of their tendency to associate more frequently with certain individuals than with others (Fig. 4), adult females were separated in two groups (A and B). A minimal AC of 30 was used as criterion to place an individual in these groups. Three individuals, however, had average ACs of 30 or more with both groups. In these cases their degree of association with the subadults of each group was taken into account. Wells *et al.* (1987) found a similar pattern of association among bottlenose dolphin females in Sarasota Bay, Florida and they were called 'bands'. The average AC was 51 (S.D.=12) among females in Band A and 49 (S.D.=15) among females in Band B. The difference was not statistically significant ($F_{1,148}=0.20$, $P>0.05$). The average AC among all females in both bands was 39 (S.D.=19).

Some females formed very stable associations, creating cores within the bands. For example, in Band A individuals #23, #26, #58, and #100. They had an average AC of 77.5. Other females frequently sighted together in Band A were #223, #25 and #50, with an average AC of 70. In Band B individuals #13, #103, #375 and #255 had an average AC of 60.

Both female bands showed preference for different sites within the community home range. Groups containing only females from Band A were observed more frequently in the northern part (Río Hondo) than in the central part (Puná Vieja)

| | | | |
|-----|----|-----|-----|
| | 59 | 108 | 109 |
| 59 | | | |
| 108 | 48 | | |
| 109 | 48 | 96 | |

Figure 6. Association values among identified males.

other pair of dolphins with a similar high degree of relatedness as #108 and #109 was found in community #2. However, two other pairs of big adults, presumably males, with similar high AC were found in communities #1 (inds. #3 and #37, AC=81) and #3 (inds. #42 and #125, AC=81).

Associations among adult females and subadults

Adult females and subadults (Fig. 7) in Band A had a significant higher degree of association (AC=44, S.D.=13) than in Band B (AC=38, S.D.=14)

($F_{1,152}=6.59, P<0.05$). In Band A subadults #67, #65, #49 had a high AC with adult females #58, #50, #25 and #100. In another case, subadult female #F32 had a high AC with females #58 and #26 (76). Similar results were observed in Band B among subadult #381 and females #375, #255 and #369. Adult females in Band A showed a low AC with subadults from Band B (17, S.D.=10) and adult females from Band B even showed a low AC but slightly higher with subadults from band A ($X=22, S.D.=13$). The average AC among adult females and subadults was 34 (S.D.=17).

There was no significant difference between the ACs shown by subadult females with adult females and unsexed subadults with adult females in band A ($F_{1,134}=0.11, P>0.05$) nor in band B ($F_{1,16}=1.06, P>0.05$). This suggests either that subadults of both sexes associated equally with adult females or that most of the animals recorded as subadults are females.

| | | SUBADULTS | | | | | | | | | | | |
|----------------------------|---------------------------------|-----------|----|----|-----|-----|----|-----|-----|-----|-----|------|----|
| | | A | | | | | | | | | B | | |
| | | 67 | 65 | 49 | F32 | F24 | 55 | 242 | 256 | 381 | 237 | F272 | |
| A D U L T S | 58 | 65 | 64 | 59 | 76 | 53 | 67 | 34 | 35 | 23 | 7 | 14 | |
| | 50 | 72 | 61 | 67 | 43 | 54 | 59 | 57 | 27 | 24 | 7 | 7 | |
| | 25 | 68 | 63 | 51 | 33 | 46 | 34 | 53 | 25 | 28 | 21 | 20 | |
| | 100 | 69 | 53 | 62 | 58 | 42 | 43 | 33 | 33 | 20 | 9 | 8 | |
| | 223 | 63 | 58 | 48 | 42 | 42 | 52 | 42 | 33 | 40 | 9 | 17 | |
| | 26 | 57 | 53 | 55 | 75 | 42 | 35 | 25 | 33 | 33 | 0 | 25 | |
| | 23 | 63 | 58 | 63 | 59 | 28 | 46 | 22 | 29 | 24 | 8 | 15 | |
| | 96 | 50 | 52 | 47 | 40 | 53 | 50 | 40 | 32 | 26 | 8 | 40 | |
| | 16 | 55 | 62 | 56 | 47 | 51 | 24 | 35 | 29 | 40 | 18 | 18 | |
| | 84 | 55 | 47 | 52 | 36 | 52 | 48 | 36 | 38 | 14 | 10 | 9 | |
| | 66 | 44 | 43 | 54 | 57 | 47 | 50 | 19 | 27 | 15 | 0 | 19 | |
| | 41 | 56 | 57 | 38 | 38 | 36 | 32 | 38 | 31 | 26 | 19 | 25 | |
| | F E M A L E S | 63 | 55 | 47 | 30 | 45 | 39 | 29 | 45 | 38 | 29 | 10 | 9 |
| | | 240 | 54 | 51 | 32 | 46 | 34 | 32 | 31 | 40 | 25 | 8 | 23 |
| | | 30 | 40 | 35 | 33 | 53 | 38 | 33 | 21 | 31 | 8 | 0 | 11 |
| 33 | | 40 | 30 | 33 | 21 | 36 | 44 | 21 | 31 | 16 | 11 | 11 | |
| 366 | | 46 | 36 | 48 | 17 | 42 | 26 | 50 | 33 | 40 | 9 | 17 | |
| B | | 255 | 42 | 45 | 33 | 30 | 43 | 17 | 27 | 19 | 51 | 39 | 43 |
| | | 13 | 46 | 41 | 42 | 14 | 38 | 22 | 29 | 9 | 47 | 15 | 14 |
| | 375 | 32 | 29 | 31 | 15 | 33 | 15 | 30 | 0 | 67 | 23 | 30 | |
| | 103 | 37 | 38 | 32 | 13 | 29 | 19 | 31 | 8 | 42 | 26 | 25 | |
| | 280 | 11 | 13 | 21 | 8 | 30 | 17 | 8 | 0 | 47 | 52 | 33 | |
| | 369 | 12 | 19 | 7 | 0 | 19 | 10 | 9 | 0 | 50 | 38 | 36 | |

Figure 7. Association values among adult females and subadults.

| | | FEMALES | | | | | | | | | | | | | | | | | | | | | | |
|---|-----|---------|----|----|----|----|----|----|-----|----|----|-----|-----|----|----|-----|----|----|-----|-----|-----|-----|-----|----|
| | | A | | | | | | | | | | | | | | B | | | | | | | | |
| M | | 41 | 25 | 16 | 58 | 50 | 84 | 96 | 100 | 23 | 66 | 240 | 223 | 26 | 63 | 366 | 30 | 33 | 255 | 103 | 375 | 369 | 280 | 13 |
| A | 59 | 35 | 36 | 54 | 51 | 38 | 44 | 41 | 53 | 54 | 46 | 25 | 32 | 37 | 44 | 37 | 24 | 24 | 39 | 43 | 29 | 56 | 32 | 29 |
| L | 108 | 56 | 54 | 42 | 34 | 39 | 35 | 37 | 29 | 27 | 26 | 41 | 33 | 29 | 25 | 24 | 22 | 16 | 40 | 36 | 36 | 20 | 29 | 26 |
| E | 109 | 52 | 50 | 42 | 34 | 39 | 35 | 32 | 29 | 27 | 31 | 36 | 33 | 29 | 20 | 19 | 22 | 16 | 36 | 36 | 31 | 20 | 24 | 26 |
| S | | | | | | | | | | | | | | | | | | | | | | | | |

Figure 8. Association values among adult males and adult females.

| | | SUBADULTS | | | | | | | | | |
|---|-----|-----------|----|------|-----|----|------|-----|-----|-----|-------|
| | | A | | | | B | | | | | |
| M | | 65 | 67 | F 24 | 242 | 49 | F 32 | 256 | 381 | 237 | F 272 |
| A | 59 | 53 | 51 | 58 | 33 | 49 | 39 | 27 | 29 | 23 | 14 |
| L | 108 | 56 | 43 | 33 | 45 | 27 | 20 | 12 | 26 | 21 | 20 |
| E | 109 | 56 | 43 | 33 | 40 | 27 | 20 | 12 | 22 | 21 | 20 |
| S | | | | | | | | | | | |

Figure 9. Association values among adult males and subadults.

Association among adult females and adult males

The ACs among adult males and adult females ranged between 16 and 56 (Fig. 8). The average AC between these two classes was 35 (S.D.=10). Adult males did not preferentially associate with any particular female band; none of the ANOVA tests carried out between every male and each band of females resulted in a significant difference ($F_{1,21}=0.23$, $F_{1,21}=0.55$, $F_{1,21}=0.13$, $P>0.05$). However, male #59 was more frequently found with adult females in both bands (AC=39) than were males #108 and #109 ($X=32$), a difference which was statistically significant ($F_{2,66}=4.43$, $P<0.05$). Only one of the 23 adult females had an average AC lower than 20 with the adult males (Ind. 33).

Pairs from other communities, presumed to be males for their big size and for their high AC, were seen with groups of females and calves of community #2 on 8 occasions: #42 and #125 (from community #3) 5 times, #3 and #37 (from community #1) 2 times and #235 and #236, 2 big adults from unknown origin, one.

Association among adult males and subadults

Adult males and subadults showed ACs between 14 and 58 ($X=32$, S.D.=14) (Fig. 9), a little less than between adult males with adult females but not significantly different ($F_{1,97}=0.65$, $P>0.05$). All three adult males showed ACs significantly higher with subadults of Band A ($X=37$, S.D.=14) than with subadults of Band B ($X=22$, S.D.=4) ($F_{1,28}=9.67$, $P<0.01$), but individually none of the three adult males associated more frequently with subadults than the other two ($F_{2,27}=1.03$, $P>0.05$). A significant difference was not found

in the association between adult males with subadult females nor with unknown sex subadults ($F_{1,28}=1.32$, $P>0.05$). Only two of ten subadults had an AC on average less than 20 with the adult males (#256 and #F272).

Association among mothers and calves

Except for #281, calves did not have natural marks that were distinctive enough to be recognized from photographs. During the sightings, calves were counted and identified when in association with a marked mother. Since the first time that #281 was observed, it was always observed with its mother #280 (15 times during the next 11 months). The calf was assumed to be six months old at the first sighting. The records of the other females with calves showed that at least during their first year of life, calves were always found close to their mother.

Associations with other members of the community

The form in which males, females and subadults associated with the other eleven unclassified members of community #2 is shown in Figure 10. Of these eleven animals, eight were considered to belong to Band A, two to Band B and one (#273) was not placed in any band because it had the same AC on average with both adult females and subadults in both bands. The degree of association of these eleven individuals with adult females and subadults was high; the eight individuals of Band A had an average AC of 40 (S.D.=14) with adult females and 35 (S.D.=13) with subadults, while both individuals of Band B had an average AC of 44 (S.D.=8) with adult females and 35 (S.D.=16) with subadults in their band.

UNKNOWN SEX AND CLASS ANIMALS

| | | A | | | | | | | | B | | |
|--------------------------------------|-------|----|----|----|----|-----|----|-----|----|-----|-----|-----|
| | | 94 | 52 | 27 | 29 | 367 | 72 | 239 | 68 | 273 | 234 | 448 |
| A D U L T | 23 | 52 | 54 | 72 | 38 | 43 | 42 | 26 | 29 | 9 | 18 | 33 |
| | 26 | 50 | 43 | 64 | 44 | 50 | 48 | 20 | 22 | 11 | 13 | 29 |
| | 58 | 55 | 43 | 59 | 35 | 48 | 46 | 32 | 17 | 9 | 22 | 31 |
| | 100 | 83 | 52 | 73 | 44 | 40 | 38 | 30 | 22 | 11 | 26 | 19 |
| | 66 | 57 | 60 | 53 | 40 | 47 | 33 | 35 | 27 | 13 | 14 | 22 |
| | 223 | 58 | 52 | 27 | 56 | 60 | 57 | 30 | 22 | 22 | 26 | 29 |
| | 63 | 55 | 38 | 70 | 38 | 44 | 21 | 11 | 38 | 13 | 21 | 32 |
| | 84 | 55 | 67 | 40 | 50 | 56 | 42 | 56 | 38 | 13 | 21 | 21 |
| | 50 | 50 | 52 | 31 | 45 | 42 | 48 | 25 | 18 | 18 | 23 | 16 |
| | 41 | 50 | 52 | 40 | 31 | 43 | 34 | 36 | 23 | 8 | 31 | 21 |
| | 96 | 32 | 58 | 43 | 32 | 57 | 45 | 38 | 32 | 32 | 31 | 27 |
| | 25 | 47 | 41 | 36 | 33 | 46 | 37 | 23 | 25 | 8 | 22 | 22 |
| | 240 | 58 | 40 | 33 | 30 | 45 | 43 | 27 | 20 | 10 | 36 | 26 |
| | 30 | 21 | 44 | 59 | 46 | 40 | 50 | 27 | 31 | 15 | 7 | 13 |
| | 16 | 41 | 30 | 38 | 21 | 33 | 32 | 27 | 14 | 14 | 39 | 32 |
| 33 | 32 | 56 | 24 | 46 | 40 | 63 | 27 | 15 | 31 | 15 | 0 | |
| 366 | 33 | 43 | 27 | 33 | 50 | 38 | 20 | 11 | 11 | 32 | 29 | |
| S | 255 | 22 | 33 | 23 | 13 | 42 | 18 | 24 | 6 | 19 | 50 | 41 |
| | 13 | 21 | 30 | 8 | 27 | 33 | 40 | 17 | 9 | 18 | 40 | 48 |
| | 375 | 15 | 23 | 16 | 10 | 35 | 8 | 17 | 10 | 10 | 41 | 58 |
| | 103 | 19 | 19 | 7 | 15 | 21 | 14 | 14 | 0 | 23 | 56 | 34 |
| | 280 | 8 | 17 | 9 | 0 | 20 | 10 | 20 | 11 | 11 | 52 | 38 |
| 369 | 9 | 10 | 0 | 0 | 11 | 11 | 22 | 0 | 13 | 41 | 32 | |
| A M D A U L T | 108 | 30 | 26 | 21 | 21 | 17 | 11 | 28 | 12 | 6 | 28 | 11 |
| | 109 | 30 | 21 | 16 | 16 | 11 | 11 | 28 | 6 | 8 | 28 | 5 |
| | 59 | 44 | 40 | 47 | 13 | 25 | 18 | 31 | 20 | 33 | 31 | 24 |
| S U B A D U L T | 67 | 55 | 44 | 45 | 37 | 34 | 53 | 21 | 37 | 15 | 30 | 13 |
| | 65 | 47 | 43 | 39 | 27 | 31 | 40 | 21 | 27 | 11 | 28 | 15 |
| | 49 | 52 | 62 | 56 | 29 | 43 | 50 | 17 | 38 | 19 | 24 | 15 |
| | F 32 | 45 | 29 | 60 | 25 | 33 | 32 | 11 | 25 | 0 | 14 | 21 |
| | F 24 | 32 | 47 | 48 | 16 | 30 | 43 | 22 | 32 | 24 | 37 | 14 |
| | 55 | 48 | 60 | 32 | 40 | 35 | 44 | 12 | 53 | 13 | 44 | 11 |
| | 242 | 36 | 29 | 30 | 25 | 22 | 11 | 22 | 25 | 13 | 21 | 21 |
| 256 | 25 | 27 | 29 | 20 | 33 | 31 | 50 | 0 | 40 | 9 | 0 | |
| S B | 381 | 29 | 22 | 15 | 18 | 25 | 16 | 8 | 9 | 18 | 51 | 56 |
| | F 272 | 9 | 10 | 0 | 13 | 22 | 11 | 0 | 0 | 13 | 28 | 21 |
| | 237 | 10 | 20 | 11 | 0 | 24 | 11 | 24 | 13 | 13 | 43 | 11 |

Figure 10. Association values among known and known sex and age classes animals.

ten-minute long violent fight began among these four animals. When they dispersed, dolphins #3, #37, and male #59 were no longer observed. Males #108 and #109 stayed at the site and continued swimming with other dolphins. The following day #3 and #37 were observed again 25 km to the north, outside the home range of community #2.

The second occasion (21 January 1992), a group of 5–6 dolphins, in which male #59 was swimming side by side with female #375, met with another group where males #108 and #109 were present. Suddenly, #109 rapidly approached #59 and began to chase him and a violent fight started. It was not clear whether male #108 was involved in the fight because the dolphins moved away and the activities were observed from a distance. The fight lasted just 5 minutes, then all three animals returned to the rest of the animals and continued swimming in the same direction as one single group. Males #108 and #109 were seen swimming together again, but #59 no longer swam to the side of #375. Instead, he stayed in the rear of the group.

Discussion

The bottlenose dolphin population in the Gulf of Guayaquil is organized similarly to the bottlenose dolphin populations on the west coast of Florida. Both populations are organized in resident communities of similar size, around 115 animals in the Gulf of Guayaquil and around 100 in Sarasota Bay, Florida (Irvine *et al.*, 1981; Wells & Scott, 1990). Resident communities have a well-defined home range along 30–40 km of coast, although there is some overlap in boundaries. Their exact size could not be estimated because dolphin movements offshore are little known, but resident groups showed more restricted movements offshore than non-resident communities. Wells *et al.* (1980) estimated the home range of their studied bottlenose dolphin community in Sarasota Bay to be 85 km². It is possible that resident communities in the Gulf of Guayaquil have comparable home ranges.

In general, group composition was similar in all five communities. Most abundant were the biggest groups with all age classes represented. Groups of a single age class were rather scarce. The ‘all sub-adult’ class was the one with the least number of sightings, forming only 5% of the total number of groups observed. Usually they showed evasive behavior and, due to the lack of distinctive marks on dorsal fins, they were difficult to recognize. It is suspected that these are segregated animals, just as occurs in the bottlenose dolphins of Sarasota Bay (Wells *et al.*, 1980; Irvine *et al.*, 1981; Wells *et al.*, 1987), but the present study does not provide information that such a segregation exists in the population in the Gulf of Guayaquil. Groups from

non-resident communities were bigger than resident ones. Their seasonal presence in the area is likely related to availability and abundance of prey (Félix, 1994).

Females seemed to play a more important role in the formation and integration of the groups than males. They mainly associated with other females in bands, showing preference for different sites of the community home range. In the bands, some females formed highly stable associations or cores, around which other females associated at different rates. Although some females in community #2 showed a similar degree of association with females in both bands, in general there was a tendency to associate more often with one of them. Duffield and Wells (1991) found that female bands are formed by related animals composed of several different maternal lineages, something also found in other studied cetaceans like killer whales *Orcinus orca* (Bigg *et al.*, 1990) and pilot whales *Globicephala melas* (Amos *et al.*, 1991).

Individuals identified as subadults in community #2 showed a high affinity with both adult females and adult males. This similarity suggests that most of the recorded animals assigned to this class are females too. Moreover, three of the eleven originally identified as subadults were positively identified as females when they gave birth to calves during the last year. In the bottlenose dolphins of Sarasota Bay it was proved that young females return after a segregation period to their original bands when they reach sexual maturity (Scott *et al.*, 1990; Wells, 1991). It is possible that the subadults recorded in this study were at this stage.

Adult males did not show preference for any particular female band, rather they seemed to move among bands searching for receptive females. This search would sometimes spread out beyond the limits of their communities, as suggested by the presence of pairs of individuals from two other communities in groups of females of community #2. This was also observed in Sarasota Bay dolphins, where in addition, it was reported that adult males are the class more frequently observed in mixed groups. In this way they form the main vector of genetic exchange among communities (Duffield & Wells, 1986; Wells *et al.*, 1987; Scott *et al.*, 1990; Duffield & Wells, 1991).

Some pairs of adult dolphins formed tight associations with ACs even higher than among females. One of three of such pairs recorded was positively identified as formed by males: #108 and #109 in community #2. Presumably the other two pairs were males as well, because in addition to their high AC, they were large animals and never associated with calves during the study period. In accordance to Wells *et al.* (1987) and Connor *et al.* (1992), this type of association or alliances in pairs and

sometimes in trios are typically formed by adult males. One of the most remarkable behaviors showed by the male pair #108–#109 was the aggressive behavior toward individual #59, another adult male that did not form alliances, and towards the pair #3–#37 from another community, presumably formed by males as well. In both cases of observed aggression there was at least one known female, perhaps receptive, that previously was closely associated with one of the animals involved in the fight that began when the males #108 and #109 showed up. These facts support the theory of Wells (1991) who suggested that this type of association in pairs gives cooperative males advantages during agonistic interactions with other males in order to secure a mate. Connor *et al.* (1992) also reported that pairs or trios of males cooperate in order to herd females or to rob them from other males in bottlenose dolphins in Shark Bay, Australia. If such associations serve to keep away other males from receptive females then these males would be performing some kind of dominance in the community and get a major reproductive success.

The belief that males #108 and #109 are dominant within community 2 is supported by three other facts: (1) No other association of this type was recorded in this community. It is not discounted that there were other cooperative males; however they probably did not accompany females as frequently as the dominant pair #108–#109. Wells *et al.* (1987) and Connor *et al.* (1992) reported the presence of more than one of these cooperative pairs or trios in the communities they studied; (2) When pairs of individuals from other communities, presumably males, were observed with groups of females of community #2, males #108 and #109 were absent. Apparently those presumed pairs of males took advantage of the absence of the pair #108–#109 in order to join groups of females. The only time when the pair #108–#109 was present, one of the previously described fights occurred; and (3) In spite of the fact that male pair #108–#109 was seen three times more ($n=28$) than the pair #42–#125 and twice more than #3–#37, it never was sighted outside the home range of its community, neither was it seen in groups of females from other communities. If #108 and #109 are dominant in community #2, it is likely more advantageous to defend access to females in their own communities rather than attempt access to females in other communities. The other two pairs of presumed males that frequented groups of females in the community #2 possibly were not dominant in their communities and had to look for females elsewhere.

It has been stated that hierarchy dominance is the form of social organization of the bottlenose dolphins in captivity (McBride & Hebb, 1948; Tavalga, 1966; Tayler & Saayman, 1972; Wells

et al., 1980; Shane *et al.*, 1986; Samuels *et al.*, 1991). Usually, the biggest male is dominant over the rest of the members of the group and his dominance is demonstrated with aggression toward other males during periods of sexual activity (McBride & Hebb, 1948; McBride & Kritzler, 1951; Wells *et al.*, 1980). Observations of fighting males among wild males in the Gulf of Guayaquil and similar fights observed among pairs or trios of males in Sarasota Bay (Wells, 1991) and in Australia (Connor *et al.*, 1992) support the hypothesis that a similar hierarchy dominance could be present in wild bottlenose dolphins as well. However, in contrast to what has been shown in captivity, in free-ranging dolphins dominance seems to be shared by pairs or perhaps trios of adult males. Such dominant pairs have not been observed in captivity because this type of alliance is often formed when the animals are young and perhaps it occurs more among genetically related individuals (Scott *et al.*, 1990; Wells, *et al.*, 1987; Wells, 1991). Moreover, captive animals usually come from different places. There are two reported cases of two male bottlenose dolphins that were captured together and maintained in captivity. They did not show aggressive behavior toward each other to obtain access to females (McBride, 1940, cited by Wells *et al.*, 1980; Tayler & Saayman, 1972). Wells *et al.* (1980) suggested that segregation of subadult males in wild bottlenose dolphins would be related to adult males' dominance over subadults. If this is so, whilst subadult males do not develop cooperative associations in pairs or trios, they will not be able to compete with dominant males for females.

Similar alliances among males are also present in many species of primates with striking hierarchy dominance such as macaques, baboons, chimpanzees, etc., to improve their hierarchical status to have access to receptive females or to defend their mates from other young males (Smuts, 1987). In all these cases male alliances are part of a reproductive strategy directed to obtain the highest reproductive benefit. Communities with hierarchy dominance based in male alliances seem to be common in bottlenose dolphin and some primate societies.

The presence of only one pair of cooperative adult males recorded in every studied community suggests that hierarchy dominance is more conspicuous in this tropical population than in the temperate ones. This could be related to the timing of reproduction. In Florida or Australia, seasonal reproduction occurs and several females become receptive in a short period, allowing more than one of these cooperative pairs of males to mate simultaneously with different females in the same community. Preliminary genetic studies of paternity in the Sarasota Bay dolphins indicated that several different mature males, older than 20, had sired

calves in that community (Duffield and Wells, 1991; Duffield *et al.*, 1991; Wells, 1993). However, in tropical zones where reproduction occurs with the same intensity all year long (see Perrin *et al.*, 1976; Félix, 1994), the same pair of dominant males could successfully mate with a greater number of females by concentrating their activities around, and defending access to, the female bands in the community. Therefore, bottlenose dolphins in the Gulf of Guayaquil, and perhaps in other tropical habitats as well, seem to be polygynous, with a pair of dominant males siring most of the calves in the community. Genetic studies of paternity could be an important tool to determine how successful this reproductive strategy is and under what environmental and social conditions that can allow males to monopolize females.

Acknowledgements

I would like to thank all FEMM members and friends who accompanied me during the trips. Ben Haase and Rebecca Glaab helped me with the translation of the Spanish version. Several colleagues contributed sending papers. Michael Scott reviewed the manuscript and made valuable comments.

References

- Amos, B., Barrett, J. & Dover, G. A. (1991) Breeding system and social structure in the Faroese pilot whale as revealed by DNA fingerprinting. *Rep. Int. Whal. Commn. (Special Issue 13)*, pp. 255–268.
- Bigg, M. A. (1982) An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. Int. Whal. Commn.* **49**, 227–267.
- Bigg, M. A., Olesiuk, P. F. G., Ellis, M., Ford, J. K. B. & Balcomb, K. C. (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Commn. (Special issue 12)*, pp. 383–405.
- Ballance, L. (1990) Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California. In: S. Leatherwood & R. Reeves (eds). *The Bottlenose Dolphin*. pp. 267–283. Academic Press: San Diego, 653 pp.
- Cairns, S. J. & Schwager, S. J. (1987) A comparison of association indices. *Animal Behaviour* **35**, 1454–1469.
- Connor, R. C., Smolker, R. A. & Richards, A. F. (1992) Dolphin alliances and coalitions. In: A. M. Marcourt & F. B. M. de Waal (eds). *Coalitions and Alliances in Humans and Other Animals*. pp. 415–443. Oxford Science Publications.
- Duffield, D. A. & Wells, R. S. (1986) Population structure of bottlenose dolphins: genetic studies of bottlenose dolphins along the central west coast of Florida. Contract Report to National Marine Fisheries Service, Southeast Fisheries Center. Contract N0. 45-WCNF-5-00366. 16 p.
- Duffield, D. & Wells, R. S. (1991) The combined application of chromosome, protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. *Rep. Int. Whal. Commn. (Special Issue 13)*, pp. 155–169.
- Duffield, D. A., Wells, R. S., Scott, M. D., Chamberlin-Lea, J. & Sheehy. (1991) Paternity in a free-ranging bottlenose dolphin society. *Ninth Biennial Conference on the Biology of Marine Mammals*. December 5–9, 1991. Chicago, U.S.A., pp. 19 (abstract).
- Félix, F. (1994) Ecology of the bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Ecuador. *Investigations on Cetacea* **25**, 235–256.
- Heimlich-Boran, J. R. & Heimlich-Boran, S. L. (1990) Occurrence and group structure of short-finned pilot whales *Globicephala macrorhynchus* off the western coast of Tenerife, Canary Islands. *Proc. Fourth Ann. Conf. European Cetacean Society*. Palma de Mallorca 2–4 March 1990, pp. 102–104.
- Irvine, A. B., Scott, M. D., Wells, R. S. & Kaufmann, J. H. (1981) Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* **79**(4), 671–688.
- McBride, A. F. (1940) Meet Mr. porpoise. *Nat. Hist.* **45**, 16–29.
- McBride, A. F. & Hebb, D. O. (1948) Behavior of the captive bottlenose dolphin *Tursiops truncatus*. *J. Comp. Physiol. Psychol.* **41**, 111–123.
- McBride, A. F. & Kritzler, H. (1951) Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, **32**, 251–266.
- Norris, K. S. & Dohl, T. P. (1980) Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bulletin, U.S.* **77**, 821–849.
- Perrin, W. F., Coe, J. M. & Zweifel, J. R. (1976) Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fishery Bulletin* **74**(2), 229–269.
- Saayman, G. A. & Tayler, C. K. (1979) The Socioecology of humpback dolphins. In: H. E. Winn & B. L. Olla (eds). *Behavior of Marine Animals, Vol. 3. Cetacea*. pp. 165–226. Plenum Press: New York, 438 pp.
- Samuels, A., Clifford, T., Sevenich, M. & Sullivan, T. (1991) Dominance relations of bottlenose dolphins. *Ninth Biennial Conference on the Biology of Marine Mammals*. December 5–9, 1991. Chicago, U.S.A., pp. 61 (abstract).
- Scott, M. D., Wells, R. S. & Irvine, A. B. (1990) A long-term study of bottlenose dolphins on the west coast of Florida. In: S. Leatherwood & R. Reeves (eds). *The Bottlenose Dolphin*. pp. 235–244. Academic Press: San Diego, 653 pp.
- Seber, G. A. F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Griffin: London, 654 pp.
- Shane, H. S., Wells, R. S. & Würsig, B. (1986) Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science* **2**(1), 34–63.
- Smuts, B. B. (1987) Sexual Competition and Mate Choice. pp. 385–399. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (eds). *Primate Societies*. The University of Chicago Press: Chicago, 578 pp.

- Stevenson, M. R. (1981) Variaciones estacionales en el Golfo de Guayaquil, un estuario tropical. *Boletín Científico y Técnico del Instituto Nacional de Pesca de Ecuador* **4**(1), 5–32.
- Tayler, C. K. & Saayman, G. S. (1972) The social organization and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. *Annals of the Cape Provincial Museum (Natural History)* **9**, 11–41.
- Tavolga, M. C. (1966) Behavior of bottlenose dolphins (*Tursiops truncatus*): social interactions in a captive colony. In: K. S. Norris (ed.). *Whales Dolphins and Porpoises*. pp. 718–730. University of California Press: Berkeley, CA.
- Wells, R. S. (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: K. Pryor & K. Norris (eds). *Dolphin Societies, Discoveries and Puzzles*. University of California Press: Berkeley, CA, 397 pp.
- Wells, R. S. (1993) Parental investment patterns of wild bottlenose dolphins. In: N. F. Hecker (ed.). *Proceedings of the 18th International Marine Animal Trainers Association Conference*, November 4–9, 1990. pp. 58–64. Chicago, U.S.A.
- Wells, R. S. & Scott, M. D. (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Rep. Int. Whal. Comm. (Special Issue 12)*. pp. 407–415.
- Wells, R. S., Irvine, A. B. & Scott, M. D. (1980) The social ecology of inshore odontocetes. In: L. M. Herman (ed.). *Cetacean Behavior*. pp. 263–317. Wiley-Interscience: New York, 463 pp.
- Wells, R. S., Scott, M. D. & Irvine, A. B. (1987) The social structure of free-ranging bottlenose dolphins. In: H. H. Genoways (ed.). *Current Mammalogy. Vol I*. pp. 247–305. Plenum Press: New York and London.
- Würsig, B. (1978) Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. *Biological Bulletin* **154**, 348–359.
- Würsig, B. & Würsig, M. (1977) The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* **198**, 755–756.