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* (Norton & Dohl, 1980) and short-finned pilot whale *Globicephala macrornynchus* (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 northwestern (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 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 underestimated 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.
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, where the main survey route passes. 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 the this case was caused by a sampling artifact and not necessarily because the community was smaller.

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 the 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>
<thead>
<tr>
<th>Item</th>
<th>Communities</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Different dolphins sighted in 1990 (February 1990–January 1991)</td>
<td>25 76 85 22</td>
</tr>
<tr>
<td>(B) Different dolphins sighted in 1991 (February 1991–January 1992)</td>
<td>37 79 91 70</td>
</tr>
<tr>
<td>(C) Dolphins sighted both years</td>
<td>16 49 48 12</td>
</tr>
<tr>
<td>(D) Estimated abundance</td>
<td>56 122 160 120</td>
</tr>
<tr>
<td>C.I. 95% confidence interval</td>
<td>36–75 102–142 130–190 63–177</td>
</tr>
</tbody>
</table>
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 (F1,148=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).
Figure 3. Association matrix among identified dolphins in the community #2. F=female, M=male, S=subadult, C=calf.
(X2=5.46, P<0.025) and groups containing only females of the Band B were more frequently observed around the Puná Vieja Channel than in the northern part (X2=10.35, P<0.005). Groups containing females from both bands were observed with the same frequency in both sites (X2=0.086, P>0.25).

Associations among subadults
Subadults were also separated into two groups according to their association to each band of females (Fig. 5). Subadults from Band A had an average AC of 43 (S.D.=21), while the three subadults of Band B had an AC of 26 (S.D.=7). As among adult females, some subadults in Band A were regularly found together showing a high AC. For example, individuals #49, #67, #65 and #24 had an average AC of 70. The average AC among all subadults was 30 (S.D.=21).

Individuals #24, #32 and #272 were considered subadults for this analysis even though each gave birth to a calf during 1992, because most of their sightings were made previously to the births.

Associations among adult males
Only three adult males could be positively identified (Fig. 6). Males #108 and #109 were almost always found together with an AC of 96, even higher than among females. The other male #59 associated in lesser degree with these two males (AC=48). No
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) (F1,152=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 (F1,134=0.11, P>0.05) nor in band B (F1,16=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.

**Figure 6.** Association values among identified males.

**Figure 7.** Association values among adult females and subadults.
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 (F1,21=0.23, F1,21=0.55, F1,21=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 (F2,66=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.

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 (F1,21=0.23, F1,21=0.55, F1,21=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 (F2,66=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 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.

Association 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.
### Bottlenose dolphins in the Gulf of Guayaquil, Ecuador

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

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>94</td>
<td>52</td>
<td>27</td>
<td>29</td>
<td>367</td>
<td>72</td>
<td>239</td>
<td>68</td>
</tr>
<tr>
<td>Adult Females</td>
<td>23</td>
<td>52</td>
<td>72</td>
<td>38</td>
<td>43</td>
<td>42</td>
<td>26</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>50</td>
<td>68</td>
<td>44</td>
<td>50</td>
<td>48</td>
<td>20</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>58</td>
<td>53</td>
<td>59</td>
<td>35</td>
<td>48</td>
<td>46</td>
<td>32</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>63</td>
<td>73</td>
<td>44</td>
<td>49</td>
<td>38</td>
<td>30</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>66</td>
<td>57</td>
<td>60</td>
<td>53</td>
<td>40</td>
<td>47</td>
<td>33</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>223</td>
<td>58</td>
<td>52</td>
<td>27</td>
<td>56</td>
<td>40</td>
<td>57</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>63</td>
<td>55</td>
<td>38</td>
<td>79</td>
<td>38</td>
<td>44</td>
<td>21</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>84</td>
<td>55</td>
<td>67</td>
<td>40</td>
<td>50</td>
<td>56</td>
<td>42</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>50</td>
<td>52</td>
<td>31</td>
<td>45</td>
<td>42</td>
<td>48</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>41</td>
<td>50</td>
<td>52</td>
<td>40</td>
<td>31</td>
<td>43</td>
<td>34</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>96</td>
<td>32</td>
<td>58</td>
<td>43</td>
<td>32</td>
<td>57</td>
<td>45</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>47</td>
<td>41</td>
<td>36</td>
<td>33</td>
<td>46</td>
<td>37</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>240</td>
<td>59</td>
<td>40</td>
<td>33</td>
<td>30</td>
<td>45</td>
<td>43</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>21</td>
<td>44</td>
<td>59</td>
<td>46</td>
<td>40</td>
<td>50</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>41</td>
<td>30</td>
<td>38</td>
<td>21</td>
<td>33</td>
<td>32</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>32</td>
<td>56</td>
<td>24</td>
<td>46</td>
<td>40</td>
<td>63</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>366</td>
<td>33</td>
<td>43</td>
<td>27</td>
<td>33</td>
<td>50</td>
<td>38</td>
<td>20</td>
</tr>
<tr>
<td>Adult Males</td>
<td>255</td>
<td>22</td>
<td>33</td>
<td>23</td>
<td>13</td>
<td>42</td>
<td>18</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>21</td>
<td>30</td>
<td>8</td>
<td>27</td>
<td>32</td>
<td>40</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>375</td>
<td>15</td>
<td>23</td>
<td>16</td>
<td>10</td>
<td>35</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>103</td>
<td>19</td>
<td>19</td>
<td>7</td>
<td>15</td>
<td>21</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>280</td>
<td>8</td>
<td>17</td>
<td>9</td>
<td>0</td>
<td>20</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>369</td>
<td>9</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>11</td>
<td>22</td>
</tr>
<tr>
<td>Sub Adult Males</td>
<td>108</td>
<td>30</td>
<td>26</td>
<td>21</td>
<td>21</td>
<td>17</td>
<td>11</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>109</td>
<td>30</td>
<td>21</td>
<td>16</td>
<td>16</td>
<td>11</td>
<td>11</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>44</td>
<td>40</td>
<td>47</td>
<td>13</td>
<td>25</td>
<td>18</td>
<td>31</td>
</tr>
<tr>
<td>Sub Adult Females</td>
<td>67</td>
<td>55</td>
<td>44</td>
<td>45</td>
<td>37</td>
<td>34</td>
<td>53</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>47</td>
<td>43</td>
<td>39</td>
<td>27</td>
<td>31</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>49</td>
<td>52</td>
<td>62</td>
<td>56</td>
<td>29</td>
<td>43</td>
<td>50</td>
<td>17</td>
</tr>
<tr>
<td>F Sub Adult Males</td>
<td>32</td>
<td>45</td>
<td>29</td>
<td>60</td>
<td>25</td>
<td>33</td>
<td>32</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>32</td>
<td>47</td>
<td>48</td>
<td>16</td>
<td>30</td>
<td>43</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>48</td>
<td>60</td>
<td>32</td>
<td>40</td>
<td>35</td>
<td>44</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>242</td>
<td>36</td>
<td>29</td>
<td>30</td>
<td>25</td>
<td>22</td>
<td>11</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>256</td>
<td>25</td>
<td>27</td>
<td>29</td>
<td>20</td>
<td>33</td>
<td>31</td>
<td>50</td>
</tr>
</tbody>
</table>

| F Sub Adult Females | 381  | 29   | 22       | 15       | 18     | 25     | 16     | 8      | 9      | 18    | 51    |
|                    | 272  | 9    | 10       | 0        | 13     | 22     | 11     | 0      | 0      | 13    | 28    |
|                    | 237  | 10   | 20       | 11       | 0      | 24     | 11     | 24     | 13     | 13    | 43    |
However, there was a noticeable difference in the association among these eleven animals with adult males in respect to the other two classes. The association with the three adult males ($X=22$, $S.D.=11$) was significantly lower than with adult females or subadults ($F_{1,130}=16.17$, $P<0.01$). Also, six of these eleven unclassified individuals had an average AC of less than 20 with adult males. A possible explanation for this difference would be that some of them are males. It has been shown that young males are the class which interact less with adult males (Wells et al., 1987; Wells, 1991). On the other hand, individual #27 had a high AC with the core of females formed by #23, #26 and #100, suggesting that this individual could form part of this core of females.

### Other communities

Although the number of sightings of the other two resident communities in the study area (#1 and #4) were too few to establish individual association patterns, the results from a few individuals suggested that both communities were organized similar to community #2. Females showed stable associations characterized by high ACs and some of them were frequently found together indicating that they also would form bands. In community #1 a pair of big individuals (#3 and #37), presumably males, was observed together most of the time and sometimes they joined groups of females from other communities.

Groups from non-resident communities #3 and #5 were significantly larger than groups from resident communities ($F_{4.63}=24.6$, $P<0.01$). Individuals also formed more stable associations than resident ones; the average AC of 30 individuals from community #3 (Fig. 11) was 55 ($S.D.=16$), significantly higher than the AC of 32 ($S.D.=18$) among the residents of community #2 ($F_{1,1639}=616$, $P<0.01$). No groups of the classes ‘all adults’ or ‘all subadults’ were observed from non-resident communities.

### Aggressive behavior among males

Twice, males #108 and #109 from community #2 were observed attacking other dolphins: chasing, head-on collision, back leaps to fall over the other dolphin and other obvious and violent movements not commonly observed.

The first case occurred on 4 December 1991, when individuals #3 and #37, presumably males from community #1, stayed with a group of 10–12 dolphins from community #2, formed mainly by females with calves and in which male #59 was also present. Suddenly, these two presumed males, together with male #59, female #13 and another unidentified dolphin, began a period of intense social activity interpreted as mating behavior for approximately 45 minutes. Leaps, turns, rubbing, pursuits and other social behavior were seen during that time. Some twenty minutes after this period, two other dolphins approached from the west. Before joining the group, they could be identified as males #108 and #109. Between 100–150 m from the group, males #108 and #109 started to swim very fast towards individuals #3 and #37. Then a
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 community 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; Tavolga, 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


