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Residence Patterns, Group Characteristics, and Association Patterns of Bottlenose Dolphins Near Sanibel Island, Florida

SUSAN H. SHANE

A long-term, collaborative study of 385 individually recognizable bottlenose dolphins (*Tursiops truncatus*) near Sanibel Island in southwestern Florida revealed an open, fluid population including year-round and seasonal residents and transients. Less than 10% of the identified dolphins were seen for 10 yr or more, and new dolphins were identified throughout the study. Dolphin sightings peaked in the spring when prey species moved from the offshore Gulf of Mexico into the bays and nearshore Gulf. Group size averaged 5.5 dolphins ($n = 561$, $SD = 4.22$), and the factor which influenced group size most was the presence or absence of calves. Females were most likely and males least likely to be found in groups with calves. Associations between dolphins, measured by the simple ratio index, were generally low, indicating fluid relationships. The strongest and longest-lasting bonds were seen between pairs of males. A comparison of Sanibel dolphins with those in nearby Sarasota Bay showed that residence patterns were similar in the two areas and that apparent striking differences are likely attributable to differences between research methods and an emphasis on long-term residents in Sarasota Bay as compared with an emphasis on variable residence patterns at Sanibel.

Bottlenose dolphins, *Tursiops* sp., are long-lived, social mammals with a worldwide distribution. The best-studied bottlenose dolphins are those in nearshore coastal areas, and certain generalizations have been made about these populations. Residence patterns in coastal bottlenose dolphins range from transient, as in migratory dolphins along parts of the eastern United States (Barco et al., 1999) and along the open southern California coast (Hansen, 1990; Defran and Weller, 1999; Defran et al., 1999), to the stable resident communities reported in Sarasota Bay (Wells et al., 1980, 1987; Irvine et al., 1981; Wells, 1986; Scott et al., 1990; Connor et al., 2000) and the Adriatic Sea (Bearzi et al., 1997). Dolphins within a study area most commonly display a mixture of residence patterns (year-round, seasonal, and transient) (Würsig and Würsig, 1977, 1979; Würsig, 1978; Shane, 1980; Shane et al., 1986; Ballance, 1990; Bearzi et al., 1997; Weller, 1998). Coastal dolphins form small (<30), often sex-segregated, groups that are fluid in composition (Connor et al., 2000; Reynolds et al., 2000). Prey distribution, predation, and intraspecific competition for resources are thought to be key factors influencing group size and structure (Connor et al., 2000). Most dolphins have many associates (25–60) (Wells et al., 1987; Weller, 1991; Brägger et al., 1994; Feinholz, 1996; Rossbach, 1997; Quintana-Rizzo, 1999; Rossbach and Herzing, 1999), and the most enduring asso-

ciations are those between mothers and calves and between pairs of adult males (Wells, 1991; Connor et al., 1992, 2000; Smolker et al., 1992; Felix, 1997; Owen et al., 2002).

In this study I examine bottlenose dolphin residence patterns, group characteristics, and individual association patterns around Sanibel and Captiva islands in southwestern Florida for a 16-yr period (1982–98). Results are based on combined observations of two research programs: Shane and the Sarasota Dolphin Research Program (SDRP). Combining data sets improved my ability to examine bottlenose dolphin residency and group structure in several ways: 1) it increased the number of photographically identified dolphins in one study area; 2) year-round data for 1 yr (1985–86) are supplemented by both intensive annual surveys and opportunistic sightings; 3) the programs' survey times complemented each other, allowing for coverage during a larger time span; and 4) any sighting of an individually recognizable dolphin adds to the understanding of that individual's patterns. A primary focus of this article is to compare residence patterns, group characteristics, and association patterns of dolphins near Sanibel Island with those of dolphins in Sarasota Bay, a similar environment 120 km to the north (Wells, 1986, 1991; Wells et al., 1987; Scott et al., 1990). This comparison offers an opportunity to evaluate how we describe bottlenose dolphin communities and residence patterns.

Fig. 1. Bottlenose dolphin study area near Sanibel Island in southwestern Florida.

METHODS

Initial research objectives of my study and SDRP's differed, but both groups gathered data on individually recognizable dolphin group size and composition within my study area around Sanibel and Captiva islands (Fig. 1). I gathered data full time in 1985–86 (Shane, 1987, 1990a, 1990b), followed by one or two field periods each year in nine of the ensuing 10 yr (Table 1).

SDRP conducted several annual surveys of bottlenose dolphins in Charlotte Harbor and Pine Island Sound (850 km²) that encompassed my study area (Wells et al., 1996, 1997). Only SDRP sightings from within my study area are used in this article (Table 1).

Photographically identified dolphins sighted within my original study area (Shane, 1990a) were the focus of all analyses. When a group of dolphins was encountered, dorsal fins were photographed for the purpose of recognizing

TABLE 1. Effort within the Sanibel study area (140 km²) for the Shane and SDRP data sets, which were combined for this article. Under Search Effort, the months during which fieldwork was conducted during a given year are provided.

Year	Shane's search effort	SDRP's search effort
1982	None	2 boat d ^a (Oct.)
1984	None	3 boat d (Dec.)
1985	598 hr (May–Dec.)	None
1986	284 hr (Jan.–May)	None
1987	21 hr (Dec.)	None
1988	39 hr (May and Dec.)	None
1989	70 hr (Jan., April and Dec.)	None
1990	11 hr (April)	None
1991	11 hr (Oct.)	None
1992	4 hr (April)	3 boat d (Aug.)
1993	31 hr (April)	2 boat d (Aug.)
1994	16 hr (April–May and Dec.)	None
1995	6 hr (April and Dec.)	None
1996	6 hr (April–May)	28 boat d (Aug.)
1997	None	5 boat d (Aug.)
1998	None	3 boat d (June and July)
Total search/contact time	1,059 hr/524.5 hr + 38 hr/?	46 boat d/1,582 km or 90 hr/45 hr
No. of photographs used for IDs/ total no. of photographs taken	3,793/7,875	3,098/3,550

^a Boat day = one boat spent at least a portion of its survey time in the Shane study area on a given day.

individuals (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). I used ISO 64 or 200 color transparency film in a 35-mm camera with a 70-210 mm or 80-200 mm lens. SDRP used ISO 64 color transparency film with 35-mm cameras with 70-300 mm lenses. Forty-eight percent of my photographs and 87% of SDRP's were useful for individual dolphin identification (Table 1).

Dolphins were assigned to 15 categories based on the location of their identification marks (e.g., top only, leading edge, top and bottom) (modified from Urian and Wells, 1996). Every identifiable dolphin was compared with others in the appropriate category. If no match was made, I searched other categories. A dolphin was given a new identification (ID) number and added to the appropriate category if it could not be matched to any of the dolphins within the 15 categories.

There was one data record for each sighting of each identifiable dolphin ($n = 1,235$). Each data record included ID number, dolphin's name (if any), date, group number for the day, estimated age or size of the identifiable dolphin, gender, total number in the group, number of adults, number of calves, number of juveniles or subadults, whether the group was socializing (group members in nearly constant physical contact, making no forward movement and often displaying surface behaviors),

associated known individuals, and location. My locations were based on landmarks that delineated grids in my study area. The latitude and longitude at the center of each of my grids were used in the final data set, along with the latitude and longitude collected using Global Positioning System for each SDRP sighting. Seasons were divided into spring (March–May), summer (June–Aug.), fall (Sept.–Nov.), and winter (Dec.–Feb.).

Group size was defined as the maximum number of dolphins, including calves, counted in spatial proximity to one another, moving in the same direction and usually engaged in the same behavior (Shane, 1990a). When dolphins were sighted more than once per day, all sightings were used in all analyses except for calculating individual dolphin sighting frequencies (1 sighting/d used). An "associate" was defined as an animal seen in the same group. For group size analysis, I used one observation per group per day ($n = 561$ groups). Association pattern analyses were based on 74 dolphins seen five or more times during the study, and I used one observation per pair of dolphins per day ($n = 331$).

Dolphins were recorded as calves (i.e., dependents) if they were two-thirds or less the size of an adult beside whom they consistently swam. Very small calves with fetal folds (vertical black stripes on the torso) that were usually

head slapping when breathing were considered neonates. Juveniles and subadults were approximately 2 m long and swam independently.

Gender was divided into three groups: adult female, adult male, and unknown. Females were adults accompanied by a calf on at least two different days ($n = 43$) (same criteria used by Wells until recently, K. Hull, pers. comm.). Males were identified in two different ways: first, if a penis was observed ($n = 6$; three of these six were moved to the unknown category because they were calves or juveniles and subadults), or second, if an animal was an adult, never accompanied by a calf, and met some of the following criteria: 1) it was a large adult ($n = 18$); 2) it was in all-adult groups 50% or more of the time ($n = 29$); or 3) it was seen alone at least once ($n = 16$) ($n = 35$; 13 dolphins met one criterion and 22 met at least two criteria). Only my dolphins were included in this subset of males because SDRP did not collect data on these criteria. Although these criteria cannot absolutely identify a male, they indicate a high probability of a dolphin being male. Wells (1991, p. 220) identified "large, heavily scarred individuals, seen for many years without calves" as "presumed males." Fully grown adult males in Florida have been shown to be slightly longer and about one-third heavier than fully grown females (Read et al., 1993; Tolley et al., 1995; Fernandez and Hohn, 1998). In both Sarasota and Shark Bay, Australia, females with calves tend to form groups with other females with calves (Wells et al., 1987; Wells, 1991; Connor et al., 2000), suggesting that dolphins consistently in groups of all adults are more likely to be males. Shane (1977) hypothesized that dolphins seen >60% of the time in groups with calves were probably females, and those seen <40% of the time in groups with calves were likely males. Connor et al. (2000) refer to solitary adult males being seen in Sarasota, suggesting that solitary adults are more likely to be males than females. The sample size of adult males was 38. Most dolphins ($n = 304$) were in the unknown category, which included nonadults and adults of unknown gender.

The degree of association between individual bottlenose dolphins typically has been measured using the half-weight index (Cairns and Schwager, 1987) (e.g., Smolker et al., 1992; Bräger et al., 1994). Ginsberg and Young (1992) contend that the half-weight index tends to overestimate associations, and they advocate the use of the simple ratio index (SR) as the least biased. The appropriate association

index is dependent on the type of sampling and the likelihood of sighting a pair when they are together vs when they are separated. The half-weight index is least biased when pairs are more likely to be sighted when separate than when together, whereas the SR is least biased when the sample is random (Cairns and Schwager, 1987). I had two potential sources of bias in opposite directions. In the first but less frequent case, dolphins in separate subgroups within a much larger group (only 5% of all groups had >12 dolphins and 10% had >10 dolphins) were considered associated, thus possibly overestimating associations. Second and more likely, I might have failed to photographically identify both members of a co-occurring pair because of incomplete coverage or poor quality of the photograph, thus underestimating associations. In this study I present the SR because, on balance, my sample was closest to random.

$$SR = \frac{x}{x + y_A + y_B}$$

where

x = number of sightings including both dolphin A and dolphin B

y_A = number of sightings including dolphin A but not dolphin B

y_B = number of sightings including dolphin B but not dolphin A

Statistical analyses were conducted using the SAS System for Windows (version 6.11) and included general linear models for analysis of variance on unbalanced data, t-tests for pairwise comparisons of means, Pearson's correlation, regression to test multivariate hypotheses, and chi-square test. I graphically examined data to meet the assumptions of parametric statistical tests and used a log 10 transformation when necessary. Although results of a few statistical tests are based on transformed data (indicated in the Results), I report untransformed arithmetic mean values and standard deviations or standard errors. A significance level of $P < 0.05$ was set for all statistical analyses.

RESULTS

Occurrence and residence patterns.—Three hundred and eighty-five dolphins were photographically identified (Shane: 270; SDRP: 115). One hundred and twenty of my 270 dolphins (44%) were initially identified during 1985–86. I reported 126 photographically identified dol-

Fig. 2. Rate of discovering new identifiable bottlenose dolphins during a 16-yr study (1982 and 1984–98) near Sanibel Island, Florida.

phins in 1985–86 (Shane, 1987); internal matches (i.e., individual dolphins that were mistakenly identified as two different dolphins) reduced this number to 120.

Individual dolphin sightings ranged from 1 to 33 ($\bar{x} = 3.1$, $SD = 3.59$). The majority of dolphins were seen one (39%) or two (27%) times. Eighteen dolphins (5%) were seen ≥ 10 times. About 60% of the dolphins ($n = 229$) were seen in only 1 yr. Thirty-two dolphins were seen during a span (i.e., time between their first and last sightings) of ≥ 10 yr, and all but six of these were seen in the intervening years as well. Of these 32 dolphins, 12 were sighted ≥ 10 times. Of these 12, seven were adult males, one a juvenile male (early in the study), and four were adult females. Eight years was the maximum number of years any dolphin was sighted.

I examined long-term residence patterns for the 120 dolphins initially identified in the year-round study in 1985–86. Thirty-three of these dolphins were seen in only 1985 or 1986. An additional 27 dolphins were seen in both 1985 and 1986 but never again. The remaining 60 dolphins (50%) were seen in 1985–86 and again in later years.

Shane (1987) thought that the rate of discovering new dolphins was declining at the end of the 1985–86 study period (Fig. 2); however, data for the 16-yr period indicated that new dolphins were still being identified. There were large increases in new photographic identifications in 1989 and 1996, when there was an increased annual search effort (Figs. 2, 3; Table 1).

Seasonality of sightings.—Dolphin sighting frequencies were significantly higher in spring than during any other season in 1985–86 (Fig.

Fig. 3. Number of identifiable dolphins (white bars) initially sighted during each year of the study (1982 and 1984–97) (no new dolphins were seen in 1998). The annual search effort (in hr) is indicated by the black bars. The SDRP boat days were converted to hours by assuming the same 50% contact rate achieved by Shane; thus, 45 contact hr with dolphins during 46 boat d added up to a search time of 90 hr or 2 hr/boat d.

4) and throughout the study (Fig. 5). Dolphins sighted ≥ 5 times in 1985–86 were most frequently sighted in spring ($G^2 = 184.05$, $df = 108$, $P = 0.001$), as were dolphins seen ≥ 10 times ($G^2 = 43.77$, $df = 27$, $P = 0.02$). Both adult males and females seen ≥ 10 times for a span of ≥ 10 yr were seen most often in spring as well (Fig. 5) ($G^2 = 46.22$, $df = 30$, $P = 0.03$). All 11 of these well-known adult animals were seen least often in the fall (Fig. 5).

Group size.—Overall, group size averaged 5.5 individuals ($SD = 4.22$, $n = 561$, range = 1–31). Group size varied by gender: $\bar{x} = 6.9$ ($SD = 5.23$, $n = 186$) for females; $\bar{x} = 5.3$ ($SD = 4.24$, $n = 230$) for males; and $\bar{x} = 6.3$ ($SD = 4.63$, $n = 356$) for unknowns. Considering all three categories, gender exerted a significant influence on group size ($F = 6.94$, $df = 2$, 771 , $P = 0.001$). I compared group size for each pair of gender categories and found groups with males significantly different from groups with females ($t = 3.58$, $df = 414$, $P = 0.004$) and groups with unknowns ($t = -2.78$, $df = 584$, $P = 0.01$). The sizes of groups with females and groups with unknowns did not differ significantly from each other ($t = 1.39$, $df = 540$, $P = 0.17$).

Socializing groups of dolphins were larger ($\bar{x} = 8.2$, $SD = 4.90$, $n = 123$) than those not socializing ($\bar{x} = 4.7$, $SD = 3.66$, $n = 438$) ($t = -8.79$, $df = 559$, $P = 0.00001$).

Groups containing calves were larger ($\bar{x} =$

Dolphins Seen 5+ Times

1985-86

Dolphins Seen 10+ Times

1985-86

Search Hours 1985-86

Fig. 4. Seasonal frequency of sighting identifiable dolphins seen 5+ or 10+ times during the one full-time year of research (1985–86). Seasonal search effort (hours) is given for 1985–86.

7.6, $SD = 4.89$, $n = 252$) than groups with no calves ($\bar{x} = 3.7$, $SD = 2.47$, $n = 309$) ($t = -12.23$, $df = 559$, $P = 0.00001$). There was a strong correlation between the number of calves (range = 0–6) and the total number of dolphins (range = 1–31) in a group (Pearson = 0.67, $n = 561$, $P = 0.0001$).

Examining gender (male and female only), socializing, and presence of calves simulta-

neously, I found that only socializing ($t = 6.32$, $P = 0.0001$) and presence of calves ($t = 8.45$, $P = 0.0001$) exerted statistically significant effects on group size, whereas gender ($t = -1.56$, $P = 0.12$) did not. Further evaluation of group size, considering only socializing status and calf presence ($F = 126.70$, $df = 2$, 560 , $P = 0.0001$), showed that group size was an average of 3.7 ($SE = 0.30$) individuals larger when calves were present ($t = 12.45$, $P = 0.0001$) and an average of 3.3 ($SE = 0.36$) individuals larger when socializing ($t = 9.07$, $P = 0.0001$).

Gender was significantly associated with the presence or absence of calves in a group ($\chi^2 = 120.1$, $df = 2$, $P = 0.001$, $n = 776$) (Table 2). Females were most likely to be found in groups with calves, whereas males were least likely to be found in groups with calves.

Association patterns.—Each dolphin had 0–69 associates ($\bar{x} = 17.3$, $SD = 12.84$, $n = 74$). There was a strong correlation between the number of associates and the number of times an individual was sighted (range = 5–34 for this analysis) (Pearson = 0.45, $n = 74$, $P = 0.0001$). The only dolphin with no associates was a juvenile male (SS025) seen alone on four occasions and once in a widely dispersed group with three other independently feeding dolphins. An adult female (SS016) was the individual with the highest number of associates. There was no difference in mean number of associates based on gender category ($F = 0.83$, $df = 2$, 73 , $P = 0.44$). Females had 4–69 associates, males had 3–41 associates, and unknowns had 0–43 associates.

Associations between pairs of dolphins using the SR ranged from 0.02 to 1.0 ($\bar{x} = 0.087$, $SD = 0.086$, $n = 331$). The SR did not vary significantly by gender ($F = 2.43$, $df = 3$, 328 , $P = 0.09$).

Looking only at the maximum SR for each dolphin, I found that the mean for males ($\bar{x} = 0.283$, $SD = 0.218$, $n = 29$) was nearly 2.5 times higher than that for females ($\bar{x} = 0.117$, $SD = 0.051$, $n = 24$) ($F = 6.78$, $df = 2$, 85 , $P = 0.0018$; log 10-transformed data).

I identified the closest associate for 73 dolphins. Some dolphins had more than one equally close associate, leading to a sample size of 88. Table 3 shows the variation in the SR for each pair of closest associates based on gender. Gender significantly affected the SR of closest associates ($F = 5.41$, $df = 5$, 82 , $P = 0.0002$; log 10-transformed data). To better examine the source of variation in SR between gender pairs, I used only the four gender pairings with

Long-Term Female Seasonality 1982-98

Long-Term Male Seasonality 1982-98

Search Hours 1982-1998

Fig. 5. Seasonal frequency of sighting four females and seven males seen ≥ 10 times over the long term (≥ 10 yr). Seasonal search effort (hours) is given for the entire study, 1982–98.

the largest sample sizes (female-unknown, male-male, male-unknown, unknown-unknown) and was able to see that the differences in SR ($F = 5.24$, $df = 3, 71$, $P = 0.0025$) were attributable to differences in SRs for male-unknown pairs vs female-unknown pairs (Tukey's = 4.564, $\alpha = 0.01$; log 10-transformed data). These findings, in turn, help identify pairs with males as significantly different in SR from pairs with females because the unknowns are equivalent in the pairings.

Ten pairs of dolphins had SRs of 0.333 or higher. These pairs included 19 individuals or 26% of the dolphins whose associations were calculated. None of these most closely associated dolphins was a female. Twelve of the 19 (63%) individuals involved in these pairs were males, and the remaining seven were of unknown gender.

TABLE 2. Percentage of sightings of bottlenose dolphins in each gender category in groups with or without calves.

Gender category	Sample size	Groups with calves (%)	Groups without calves (%)
Females	188	81	19
Males	231	28	72
Unknown	357	49	51

To test whether these pairs were present in the study area year-round or just seasonally, I examined the seasonality of the sightings of the 12 individuals in the six pairs seen together in more than 1 yr. Five of these dolphins were seen year-round during both the full year of study (1985–86) and during the entire study (1985–96). Two additional dolphins were seen in all seasons during 1985–96. Other seasonal patterns for these dolphins included presence in 1) fall, winter, and spring (1 in 1985–86 and 3 in 1985–96); 2) winter and spring (4 in 1985–86); 3) fall and spring (1 in 1985–86); and 4) fall only (1 in 1985–86).

The longevity of the affiliation between these six closely associated pairs varied from 4 yr to more than 11 yr. The two pairs seen together for more than 11 yr involved four males. Two other male-male pairs were seen together in 4 yr: Two pairs, each including one male and one unknown, were seen together in 6 and 4 yr, respectively. In each case the unknown was an adult who was seen only with other adults on at least three of its sightings. The estimates of affiliation longevity are minimums because one member of a pair might have been present but not photographically identified during a particular sighting.

DISCUSSION

Occurrence and residence patterns.—Sanibel dolphins have an open, fluid population, includ-

TABLE 3. Associations between pairs of bottlenose dolphins by gender, using mean simple ratio index (SR).^a

Genders of Pair	n	$\bar{x}$ Max SR (SD)
f	9	0.108 (0.027)
fm	4	0.105 (0.03)
fu	21	0.128 (0.068)
mm	18	0.282 (0.175)
mu	21	0.313 (0.272)
uu	15	0.159 (0.088)

^a Gender abbreviations: f = female; m = male; u = unknown.

ing both seasonal and year-round, long- and short-term residents and transients, based on the following: the large range in number of sightings per dolphin (1–33), the low mean number of sightings per dolphin ($\bar{x} = 3.1$), the high percentage (51%) of dolphins seen only once or twice in 1985–86 and never seen again, <10% of the identifiable dolphins (32/385) being seen during a span of ≥ 10 yr, and the continuing upward trend in discovery of new identifiable dolphins. The mixture of residents and transients at Sanibel is by far the most commonly reported occurrence pattern for bottlenose dolphins studied year-round in numerous locations, including Argentina (Würsig and Würsig, 1977; Würsig, 1978); eastern Australia (Lear and Bryden, 1980); Texas (Shane, 1980; Bräger, 1993; Fertl, 1994; Weller, 1998; Maze and Würsig, 1999; Irwin and Würsig, 2004); California (Hansen, 1990); South Africa (Peddemors, 1993); western Australia (Smolker et al., 1992); Mexico (Ballance, 1990); Ecuador (Felix, 1997); Scotland (Wilson et al., 1997); Cedar Keys, Florida (Quintana-Rizzo, 1999; Quintana-Rizzo and Wells, 2001); and South Carolina (Zolman, 2002).

Dolphin sightings at Sanibel peaked during spring, when prey species concentrated in the bays and nearshore Gulf (Harris et al., 1983; Barros and Odell, 1990; Shane, 1990b; Barros and Wells, 1998). Seasonal changes in abundance occur in other areas (Shane, 1980; Shane et al., 1986; Fertl, 1994; Wilson et al., 1997), but this study provides the first documentation for such changes on the West Coast of Florida. Dolphins in Sarasota concentrate in bays and nearshore waters during April–Sep., but no seasonal change in sighting frequency was noted there (Connor et al., 2000).

Group size.—The average group size at Sanibel was about five dolphins, which is consistent with that seen in other studies of coastal bottlenose dolphins in temperate bays and nearshore waters (Connor et al., 2000). The presence or absence of calves had the greatest effect on group size, and females formed larger groups than did males, as has been found elsewhere (Scott et al., 1990). Socializing dolphins formed larger groups than did non-socializing dolphins, as was found in Texas by Shane (1977) and Fertl (1994) and earlier at Sanibel (Shane, 1987, 1990a). Maze-Foley and Würsig (2002) hypothesized that larger groups seen in San Luis Pass, Texas, in spring were linked to increased socializing and a peak in calving at that time.

Association patterns.—Sanibel dolphins had an average of 17 associates, a number that did not vary by gender and was much lower than that in other studies (Wells et al., 1987; Weller, 1991; Bräger et al., 1994; Feinholz, 1996; Rossbach, 1997; Quintana-Rizzo, 1999). Other studies often put a higher threshold number of sightings per individual (e.g., 15 or 20) than I did (5) for inclusion in the data set analyzing the number of associates. Because I had a smaller pool of sightings to examine, this may have limited my number of associates as well. I have no reason to believe that Sanibel dolphins actually have fewer associates than do dolphins in other areas.

Overall, dyad associations at Sanibel were low ($\bar{x}$ SR = 0.087). The highest pairwise associations were between adult males, as has been observed in locations as widespread as Florida, Australia, and Ecuador (Wells, 1991; Connor et al., 1992; Smolker et al., 1992; Felix, 1997; Owen et al., 2002), showing that this aspect of bottlenose dolphin social organization is common. Strong bonds between pairs and trios of males have been attributed to improved reproductive success (Wells, 1991; Connor et al., 1992; Felix, 1997) or to better chances of success in aggressive interactions (Wells, 1991; Felix, 1997). Owen et al. (2002) contend that the male pair bond is the dominant male reproductive strategy for bottlenose dolphins. Predation could be a factor influencing whether pair or trio formation for males is more beneficial than being solitary (Connor et al., 2000).

Female association patterns seemed to differ between Sanibel and Sarasota. At Sarasota, consistent and relatively high associations were seen in clusters of females, which were called bands (Wells et al., 1987). At Sanibel there was no convincing evidence for female bands. Females at Sanibel had a larger range in number of associates than did males, and at Sarasota females also show a broad range in sociability, from relatively solitary to being typically found in groups (Connor et al., 2000).

Comparing Sanibel and Sarasota Bay.—The most striking difference between dolphins at Sanibel and Sarasota is found in residence patterns. All data pointed to an open, fluid population at Sanibel, whereas the Sarasota Bay dolphins are described as a long-term resident community of about 100 (Wells et al., 1987; Connor et al., 2000). I looked at habitat, study area boundaries, and research effort and methods to explain the apparent difference in residence patterns between Sanibel and Sarasota dolphins.

The Sanibel and Sarasota study areas are very similar: 40 km along Florida's Gulf coast including shallow estuaries with barrier islands, mangroves, seagrass flats, dredged channels, nearshore Gulf waters, abundant boats, and considerable human development onshore. The only notable difference between the two study areas is that the Sarasota area is only accessible to the Gulf through three narrow passes, whereas the Sanibel area connects with the Gulf through a large (4 km wide) pass, as well as two narrow passes. Smolker et al. (1992) proposed that narrow passes in Sarasota might permit territorial defense, which would be impossible in more open habitats like Shark Bay, Australia, and Sanibel. Actually, the Sarasota community home range extends a few kilometers into the Gulf of Mexico (Wells, 1991), making the passes irrelevant as range boundaries. Shane (1987) noted that the Sanibel area may have included part or all of at least two community ranges. Since then, I (unpubl. data) identified 14 different home ranges used by subsets of the 270 dolphins I identified. The largest pass at Sanibel's eastern end did serve as a home-range boundary for some dolphins, whereas other dolphins' ranges crossed through it (Shane, 1987; S. H. Shane, unpubl.). A more prominent home-range boundary that well-known dolphins rarely crossed extended across open water from Blind Pass eastward to Pine Island (Fig. 1) (Shane, 1987; S. H. Shane, unpubl.). Considering all these factors, habitat and study area boundaries fail to explain the difference in residence patterns between Sanibel and Sarasota.

Connor et al. (2000) contend that bottlenose dolphins may have many overlapping community ranges along Florida's central West Coast, as they do in western Australia. Because even the most frequently sighted Sanibel dolphins appeared to leave the study area occasionally or seasonally, I wondered where they might be going. In the past, SDRP has compared my photographically identified dolphins with those in the Sarasota Bay community and found no matches. Similarly, Quintana-Rizzo and Wells (2001) compared dolphins photographically identified in the Cedar Keys with those in Clearwater and farther south and found no matches. Thus, there is no evidence for relatively long-distance movements (≥ 120 km) by dolphins along Florida's West Coast.

I examined research effort and methods as possible influences on perceptions of dolphin residency. In the Sanibel study, there was 1 yr of full-time research, supplemented by additional surveys in different months in different

years (Table 1). Search effort data are not consistently presented for the Sarasota study, making it impossible to clearly compare the studies in terms of this variable. A couple of references to search effort in Sarasota noted 288 surveys conducted in 7.75 yr (1980–87) (an average search time of 37 d/yr) (Wells and Scott, 1988) and 200 d of survey effort from April 1980 to Jan. 1984 (Wells, 1991). This level of effort was lower than that in Sanibel; yet, the description of a resident community at Sarasota first appeared in Wells et al. (1987) based on this effort. Owen et al. (2002) stated that dolphin associations were monitored year-round in Sarasota in 1993–2000, indicating a more thorough effort in recent years.

By capturing and marking dolphins for three decades in Sarasota Bay, the SDRP team has come to recognize a far larger proportion of dolphins than I was able to using photographic identification alone. Repeated sightings of known individuals in Sarasota Bay during this time have led to the perception of a resident community. In Sarasota 49% of all dolphins sighted in 1980–84 were seen ≥ 5 times (Wells et al., 1987); in Sanibel only 20% of all dolphins were seen ≥ 5 times in 1985–98. In Sarasota, 77 repeatedly sighted dolphins accounted for 35% of sightings in 1975–84 (Wells et al., 1987). Comparatively, the 12 dolphins most frequently sighted during the long term at Sanibel accounted for 17% of all sightings in 1985–98. Interestingly, if one assumes that most dolphins at Sarasota were recognizable (because of tag scars and freeze brands as well as natural marks) and that only 50% of Sanibel dolphins were recognizable (Shane, 1987), the above percentages are equivalent because they differ by approximately a factor of two. Although research methods may have contributed to different sighting rates, it seems that when proportions of identifiable animals are accounted for, the data may not be as different as they first appear.

Finally, I closely examined the Sarasota Bay data and found a more complicated mixture of residence patterns than is conveyed by the "resident community" descriptor. Seventeen percent of Sarasota groups included dolphins not considered part of the Sarasota community (Wells et al., 1987). Connor et al. (2000) said that 75% of the individuals initially seen in 1970 remained in Sarasota as of 1995, but Wells et al. (1987) cite fewer dolphins (66%) being reidentified during a shorter period of time (early 1970s to early 1980s). Another example of significant mixing between the Sarasota dolphins and others is that more than

40% of calves born there are fathered by males living outside the Sarasota area (Owen et al., 2002). Also, some Sarasota males “disappear from the area for days to months at a time” (Connor et al., 2000, p. 103). Generally, the Sarasota area did include transients and temporary visitors as well as long-term residents (some of which may have been seasonal) just as in most other study areas around the world.

There is no rigorous definition of “community” for bottlenose dolphins. In Sarasota Bay, the term is used to describe dolphins identified and frequently sighted within a home range that coincides with the study area (Wells et al. 1987; Connor et al., 2000). At Sanibel, I observed individual home ranges that were often shared with others, but I do not necessarily consider dolphins with overlapping ranges a community. Because 11 of the 12 long-term residents at Sanibel shared San Carlos Bay as part of their home ranges (S. H. Shane, unpubl.), I could have used these animals as an example of a San Carlos Bay “community.” However, what stood out to me was the variety of residence patterns and ranges at Sanibel. In Sarasota Bay, repeated sightings of many well-known dolphins for 30 yr have caused the emphasis to be placed on long-term residents rather than on the varied occurrence patterns, which also are seen there. Residence patterns are similar at Sanibel and Sarasota but different perspectives, born of different research methods and time frames, seem to have led to a lumping approach in Sarasota Bay and a splitting approach at Sanibel.

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