Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies

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Abstract: Previous studies of Atlantic bottlenose dolphin, *Tursiops truncatus*, social structure near Sarasota, Florida, revealed two distinct patterns of ranging and association among paired and unpaired adult males. We evaluated these patterns using a longer-term dataset to examine whether they represent alternative strategies. Males were categorized as paired or unpaired based on coefficients of association using survey data collected year-round from 1993 to 2000. Longitudinal data also allowed for determination of lifetime pair-bond status, which enabled analysis of the occurrence of alternative strategies. Male associations with other males and with females of differing reproductive states were examined annually and seasonally. No significant differences were found between paired and unpaired males in either spatial or temporal patterns of association with all classes of females. Lagged association analysis shows that males tend to associate with breeding females preferentially well before the breeding season starts, suggesting that they may develop affiliative relationships with females during the nonbreeding period to influence female choice later. Paired and unpaired males differed in ranging patterns as calculated by the fixed kernel method. Paired males had significantly larger overall ranging areas (95% utilization distribution (UD)) and core areas (25% UD) than unpaired males. Although these differences were significant, additional demographic analyses of lifetime probability of pair-bond formation suggest that pair bonding is the norm among adult males and that unpaired males are a transitional stage rather than an alternative strategy.

Résumé : Des études antérieures sur la structure sociale des dauphins à gros nez, *Tursiops truncatus*, près de Sarasota, en Floride, ont révélé l’existence de deux patterns différents de dispersion et d’association chez les mâles adultes appariés et chez ceux qui ne le sont pas. Nous avons évalué ces patterns au moyen d’un ensemble de données à long terme permettant de déterminer s’il s’agit de stratégies de rechange. Les mâles ont été reconnus comme appariés ou non appariés selon les coefficients d’association déterminés d’après un inventaire effectué en permanence entre 1993–2000. Des données longitudinales ont également servi à identifier les couples unis pour la vie, ce qui a permis l’analyse de l’incidence de stratégies de rechange. Les associations des mâles avec d’autres mâles et avec des femelles de divers statuts reproducteurs ont été examinées en fonction des saisons et en fonction des années. Nous n’avons pas trouvé de différences spatiales ou temporelles significatives entre les mâles appariés et les mâles non appariés en association avec toutes les classes de femelles. Une analyse des associations avec décalage dans le temps révèle que les mâles ont tendance à s’associer de préférence aux femelles reproductrices bien avant le début de la saison de la reproduction, ce qui semble indiquer qu’ils ont des affiliations avec des femelles en dehors de la saison de la reproduction pour influencer le choix des femelles plus tard. Les mâles appariés et non appariés ont des patterns différents de choix d’un domaine, tel que révélé par la méthode des noyaux fixes (fixed kernel). Les mâles appariés ont des domaines significativement plus grands (95 % UD) que les mâles non appariés et la région centrale de leurs domaines est également plus grande (25 % UD). Bien que ces différences soient significatives, des analyses démographiques supplémentaires de la probabilité que le lien entre deux animaux appariés soit pour la vie indiquent que la formation de couples constitue la norme et que les mâles non appariés sont dans une phase de transition; il ne s’agit donc pas là d’une stratégie de rechange.

[Traduit par la Rédaction]

Introduction

Alternative reproductive behaviors, defined as "... any discontinuous variation in an aspect of reproductive behavior among one sex in a single population with associated differences in the behavior’s costs and (or) benefits” (Austad 1984), are relatively common in nature (Alonzo and Warner 2000), particularly among males. These alternatives may include...
significant behavioral, morphological, and life-history differences. While alternative strategies may be genetically determined (e.g., marine isopod, Paracerceis sculpta (Shuster and Wade 1991); swordtail fish, Xiphophorus nigrensis (Ryan et al. 1992); ruff, Philomachus pugnax (Lank et al. 1995)), the majority of alternative reproductive behaviors are classified as conditional strategies (Dominey 1984; Gross 1996; Widemo 1998). In a condition-dependent strategy, an individual adopts a tactic relative to some aspect of the individual’s status (e.g., age, size, physical condition, social standing), and the chosen tactic results in higher fitness for the individual. Alternative reproductive behaviors, and in particular condition-dependent strategies, are found in most major taxa, including mammals (reviewed in Gross 1996).

Previous research as part of a longitudinal study on a community of free-ranging Atlantic bottlenose dolphins, Tursiops truncatus, near Sarasota, Florida, has demonstrated the existence of two different social patterns for adult males (Wells et al. 1987). In this community, some adult males form long-term, stable pair bonds that last up to the duration of the males’ adult life (at least 20 years, Wells 1991). Some pair bonds may form when the members are subadults, crystallizing at sexual maturity (Wells 1991). Genetic analyses and observational data from long-term studies indicate that members of a male pair are often not closely related (Duffield and Wells 2002). Studies on Indian Ocean bottlenose dolphins, Tursiops aduncus, in Australia (Connor et al. 1992a, 1992b; Möller et al. 2001) and Atlantic bottlenose dolphins in the Bahamas (Parsons et al. 2001) have also found adult males to form strong male–male bonds. These male–male alliances have been hypothesized to increase mating opportunities. Male pairs may gain greater access to females because (i) they may range farther and therefore may encounter more females (Wells 1991), (ii) they may have an increased ability to separate or herd females from groups (Wells 1991; Connor et al. 1992a, 1992b), (iii) females may preferentially select a male if he is in a synchronized pair (Connor et al. 1992b; Trainer and McDonald 1993, 1995), (iv) paired males may outcompete other males whether in pairs or not (Connor et al. 1992a, 1992b), and (v) paired males may be able to control access to females through mate guarding (Connor et al. 1992a, 1992b; Moors 1997).

Not all adult males in Sarasota form these pair bonds, however, and previous research has described two different patterns of ranging and association: “resident” unpaired males that reside within core areas of particular bands of females and associate most frequently with those females and “roving” paired males that move over a greater area and farther outside the community range, typically having brief encounters with fewer females at any particular time (Wells et al. 1987). Initial paternity analyses have indicated that both unpaired and paired males have sired calves (Wells et al. 2001; Wells 2003).

While these and other previous studies have documented general patterns of association for adult males in Sarasota, a detailed examination of the interactions of adult males with both females and other adult males has awaited a longer-term dataset because long-term associations between individual males can span decades. The purpose of this study was to (i) describe the long-term association and ranging patterns of adult males in this community and (ii) re-examine the “resident, unpaired” versus “roving, paired” male patterns with a longer-term dataset to determine whether these patterns represent alternative strategies of theoretical evolutionary significance or whether they are simply the result of demographic and social factors.

Methods

Background on the study system

The community of bottlenose dolphins near Sarasota consists of approximately 120 individuals of four generations (Wells et al. 1987; Wells 1991) that inhabit a system of shallow bays enclosed by barrier islands and the nearshore Gulf of Mexico waters on the southwest coast of Florida (Fig. 1) (Scott et al. 1990). Through capture-release efforts, along with observations over the last 30 years, the age, sex, and (or) genetic relationships are known for more than 90% of the individuals that comprise the resident community (Wells 2003).

Dataset

For 1975–2000, the Chicago Zoological Society’s Sarasota Dolphin Research Program (SDRP) database contains 20,780 sightings of dolphin groups. Each line of sighting data includes information on date, time, location, environmental conditions, numbers and identifications of animals, and animal activities. As described below, different portions of this dataset were selected for different analyses. More than 2500 distinctive dolphin dorsal fins exist in the SDRP catalog; of these, 61 are adult males known to be resident to the Sarasota Bay area during the period considered for this study.

Measures of association

Association patterns of animals that were of known age and sex and had established sighting histories were examined. Sex determination occurred during temporary capture-release operations (Wells 1991). Ages were either determined from survey data (documented calf birth and subsequent tracking of the individual throughout life) or based on analyses of dentinal and cemental growth layer groups in teeth (Hohn et al. 1989). We used data from the SDRP database collected between 1 January 1993 and 31 December 2000, a period during which association data were recorded year-round, to (i) assign adult males to the categories of “paired” or “unpaired” and (ii) compare the spatial and temporal association patterns of paired and unpaired males with females of differing reproductive status annually and in the breeding and nonbreeding seasons. Sightings in the database that met all of the following criteria were used: (i) data were collected during standardized distribution and abundance surveys, (ii) sightings received a photograph coverage grade (PG) (Urian and Wells 1996) of either 1 (all dolphins in the group were photographed or otherwise positively identified) or 2 (there were photographs of some dolphins with distinctive fins that may be in the catalog, but because of the quality of photographs, it was not possible to make appropriate comparisons with the catalog and make a match or assign an identification), and (iii) within a survey day, if there were multiple sightings of an identical group in the same and (or) adjacent location(s) (based on physiographically defined lo-
cation codes), only the first sighting of the day of the group was considered.

For the majority of the analyses in this paper (except for calculating lagged association rates, see Temporal patterns of association section), we used sightings with PG 1 and PG 2 to increase our sample size. Including sightings with PG 2 was important to avoid a bias of focusing on groups that tended to be smaller (Baird and Whitehead 2000) because groups with PG 2 were significantly larger (mean = 5.47 individuals, SD = 4.86, n = 1487 groups) than groups with PG 1 (mean = 2.94 individuals, SD = 2.48, n = 5648 groups, p < 0.05). In sightings of PG 2, positive identifications were assigned to an average of 48.2% (SD = 28.1%) of the group members (compared with 93.3%, SD = 18.8%, for sightings with PG 1). However, because the animals of known age and reproductive status were more likely to be positively identified (as a consequence of marking and freeze-branding during temporary capture–release operations (Wells 1991)), there is a high likelihood that the majority of unidentified individuals in PG 2 sightings were those individuals of unknown age and (or) reproductive status that have never been handled and marked and therefore could not be included in these association analyses. Including PG 2 sightings did introduce bias, however, because those unidentified individuals may have included adult males or adult females, the two categories of animals analyzed in this study. However, it is likely that association patterns of these unidentified individuals mirror those of identified individuals, and this bias should therefore have been negligible. Additionally, analyses should not be conducted on unidentified individuals (Chilvers and Corkeron 2002).

In Sarasota, the breeding season is seasonally diffuse, with births predominantly occurring from May to September but peaking in June (Wells et al. 1987; Urian et al. 1996). Con-
sequentially, the breeding season was operationally defined as 15 April – 30 September and the nonbreeding season as 1 October – 14 April. This dataset enabled us to compare seven complete breeding and nonbreeding seasons over 8 years.

**Spatial patterns of association**

Coefficients of association (COAs) are representative indices of the frequency with which two individuals associate. These association indices rely on two primary assumptions: (1) physical proximity (the basis of our definition of group membership) signifies a social affiliation and (2) the amount of time that two individuals spend together is correlated with the strength of the affiliation (Bejder et al. 1998). At least the first of these assumptions is satisfied in bottlenose dolphins, where proximity, in addition to physical contact and synchronous movement, is considered to be a mechanism whereby individuals express affiliation (Connor et al. 2000). While methodological difficulties are inherent in defining a group, for the purposes of this study, we defined a group as all individuals sighted at one time that were moving in the same general direction, interacting with one another, or engaged in similar activities; typically, these animals were within an area of about 100 m in diameter and often accounted for all dolphins in sight at any given time (Wells et al. 1999). This definition enabled us to examine clusters of individuals. Because the distance between clusters was much greater than the distance between individuals within a given cluster, and because there was most often only one cluster of individuals in sight at any given time, we were unlikely to confuse members of different clusters. Consequently, we can be confident that a group sighting includes our best estimation of all animals thought to be interacting at a given point in time, thus strengthening resultant analyses of association patterns.

COAs have been particularly useful in the study of species that live in fission–fusion societies with fluid group membership (Cairns and Schwager 1987), such as ungulates, primates, and some cetacean species, including bottlenose dolphins. Several indices exist that can be used to calculate COAs (see Cairns and Schwager 1987; Ginsberg and Young 1992). The half-weight index (HWI) is the most commonly used (Whitehead and Dufault 1999) and has been previously applied in studies of bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Quintana-Rizzo and Wells 2001) and Hector’s dolphins, *Cephalorhynchus hectori* (Slooten et al. 1993). However, because the HWI tends to overestimate levels of association and its correct implementation requires the use of a maximum-likelihood estimator that can be difficult to calculate (Ginsberg and Young 1992), we selected the statistically unbiased simple ratio index, which is inherently the most accurate (Ginsberg and Young 1992; Whitehead and Dufault 1999). This index is calculated as

\[
\frac{X}{X + Y_{AB} + Y_A + Y_B}
\]

where \(X\) is the number of observation periods during which individuals A and B are observed together in the same group, \(Y_{AB}\) is the number of observation periods during which individuals A and B are both observed in separate groups, \(Y_A\) is the number of observation periods during which only individual A is observed in a group, and \(Y_B\) is the number of observation periods during which only individual B is observed in a group (Ginsberg and Young 1992). Using this index, COA values for two individuals range from 0.00 (never sighted together) to 1.00 (always sighted together).

We used SOCPROG (Whitehead 1995) to calculate COAs for all males that were at least 7 years old (most pair bonds are thought to form when males are in subadult groups between 10 and 15 years old, but Wells et al. (1987) previously reported that pair-bond formation in at least one case occurred as young as 7 years old). SOCPROG considered animals to be associated (association = 1) if they were found in the same group in the sampling period (1 day) and not associated (association = 0) if they were not seen in the same group during the sampling period (SOCPROG version 1.3 manual; Whitehead 1999). The following objective criteria were then used to define males as “paired”: (i) male has at least the average annual (or seasonal) number of sightings as all other considered males for that year (or season), (ii) minimum annual (or seasonal) COA of 0.50 with partner male, and (iii) partners are reciprocal closest associates, as measured by COA.

For those males that we defined as paired for the period 1993–2000, we used the SDRP sighting database from 1980 to 1992 and examined each year from the most recent to the earliest to determine when the pair bond was established. Once we established the year of pair-bond formation, if either member of the pair was at least 7 years of age, we examined the association patterns of that male for all years for which that male was 7 years of age or older. This allowed us to determine the minimum average age of first pair-bond formation. Additionally, for those males that were not paired from 1993 to 2000, we also examined their sighting records from 1980 to 1992 to determine whether they had previously been members of a male pair. This was the only portion of this study that used data from 1980 to 1992; all other data are from 1993 to 2000. We chose not to use data from 1980 to 1992 in our association pattern analyses because surveys were not conducted year-round during this period. Following this classification of males as paired and unpaired, COAs were calculated for male associations with females of different reproductive status (nonreproductive immature female (FNB), nonreceptive adult female (FNR), potentially receptive adult female (FPR), and adult female of unknown reproductive status (FUR)). These categories were based on calving data from the SDRP database; see Table 1 for descriptions and definitions.

**Temporal patterns of association**

While calculations of COAs provided a static “snapshot” of interactions between individuals over a specified time interval, lagged association rates (LARs) were calculated using SOCPROG (Whitehead 1995) to examine changes in association rate with time lag. LAR, for any time lag \(t\), is an estimate of the probability that two individuals interacting (or associated) at a particular time are interacting (or associating) \(t\) time units later (Whitehead and Dufault 1999). LARs were calculated for paired and unpaired males with females of differing reproductive status for 1 January 1993 – 31 December 2000 using the same criteria for sighting selection as...
Table 1. Definition of female reproductive status categories used for association-pattern analyses (based on calving histories from the longitudinal Sarasota Dolphin Research Program database).

<table>
<thead>
<tr>
<th>Female reproductive status category</th>
<th>Definition and description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nonreproductive immature female (FNB)</td>
<td>Female &lt;5 years old and independent from her mother</td>
</tr>
<tr>
<td>Nonreceptive adult female (FNR)</td>
<td>(a) Female ≤1 year before the midpoint birth date of a calf and until the beginning of the breeding season following calf birth. Although rare, females have conceived while they have a 1-year-old calf. (Because the gestation period is 12 months ± 14 days (Schroeder and Keller 1990) and the birth date is an estimate, the following rule was applied: e.g., if the female was last seen without a calf 23 August 1995 and first seen with a calf 12 September 1995, the midpoint birth date is 2 September 1995 ± 10 days (rounded up to the next whole integer). Thus, from 9 August 1994 (2 September 1994 – 24 days (10 + 14 days)) to 26 September 1994 (2 September 1994 + 24 days), female status = FUR. From 27 September 1994 to 14 April 1996, female status = FNR. And from 14 April 1996 to 30 September 1996, female status = FPR)</td>
</tr>
<tr>
<td>Potentially receptive adult female (FPR)</td>
<td>(b) If the dates are between 1 October – 14 April (nonbreeding season), and the female is ≥5 years old</td>
</tr>
<tr>
<td>Female of unknown reproductive status (FUR)</td>
<td>Adult female that cannot be assigned to any of the above categories</td>
</tr>
</tbody>
</table>

Note: If a calf dies in the first year of life before the next breeding season, a female may become receptive again in the same breeding season (female status changes from FNR to FUR to FPR; a female is categorized as FUR from the last time the female was seen with a calf to the first time the female was seen without a calf). If a calf dies in the first year of life during the nonbreeding season, female status does not change until the next breeding season.

described above, except that only sightings with PG1 were included. This modification was necessary to eliminate the need for LARs to be standardized (Whitehead 1999). Precision estimates of LARs were obtained using a jackknife procedure (Whitehead 1999).

Overall ranging and core areas

We used fixed kernels, the best estimators available for estimating home ranges (Worton 1995; Seaman and Powell 1996; Seaman et al. 1999; Powell 2000), to compare the ranging patterns of paired and unpaired adult male bottlenose dolphins. This nonparametric estimator provides a probabilistic model of home range that describes the relative amount of time that an animal spends in any one place by calculating the utilization distribution (UD) (Seaman and Powell 1996). Within their home range, animals use area disproportionately; core areas are those areas used more frequently than other areas and may contain important resources (Kaufmann 1962; Samuel et al. 1985). Using Spatial Analyst 2.0 in ArcView 3.2a, we compared the overall ranging area (95% UD) and core areas (50% UD, 25% UD) for males that we had already defined as paired or unpaired and had a minimum of 100 sightings between 1993 and 2000. This minimum number of sightings was based on Urian (2002) who found that at least 100 sightings were required to accurately estimate home range size for bottlenose dolphins in Sarasota Bay. To reduce the possibility of sighting data being autocorrelated, within any given day, if there were multiple sightings of a male (or male pair) from the same and (or) adjacent locations (based on location code), we only used the first sighting of the day from these locations. These measures of overall ranging and core areas were compared using the t test for independent samples.

Because the sighting data on which these ranging area estimates are based are intrinsically biased by survey effort, we decided to examine whether geographic locations recorded during focal animal observation periods and radio-tracking efforts (neither of which are in the SDRP-sighting database) fell within the 95% UD assigned for a particular male pair or unpaired male. Although surveys are conducted primarily within the Sarasota community range to locate individual males to carry out these focal animal observations, within an observation period, and during radio-tracking efforts, males may venture into areas not normally covered during survey efforts. Thus, because animal locations and movements obtained during either radio-tracking or focal animal observation periods are determined by the individual animal, these data inherently represent individual habitat-use patterns more accurately. Consequently, these data provide an opportunity to examine the potential effect of survey effort biases on the determination of ranging areas. Thus, for those males that met the criteria described above for examining ranging area and on which we had conducted either focal animal observations or radio-tracking in 1999 and 2000, we used geographic locations recorded 3 min apart throughout the observation periods to make this comparison.

Results

Seasonal comparison of male status

On average, 63.8% of adult males were categorized as paired and the remainder unpaired over seven breeding seasons. This did not differ from nonbreeding seasons in which 65.8% were assigned to pairs and 34.2% as unpaired. To verify whether these identified pairs of males were associating nonrandomly, permutation tests were conducted using SOCPROG (Whitehead 1995). These tests employ a slightly modified version of the procedure described by Bejder et al. (1998) and Manly (1995). Alternative datasets are randomly generated that not only maintain the same number of dol-
phins and the same number of groups as in the observed data, but the number of times each dolphin is sighted and the number of dolphins in each group are both constrained to be the same as in the observed data. Pairwise COAs are then calculated for all dyads in each of these alternative datasets. This method enables those dyads for which the COA is higher than would be expected from random association to be identified (Bejder et al. 1998) (e.g., at a significance level of 0.05, those dyads whose real COA is greater than 97.5% of their random association index are found to have significantly large associations (Whitehead 1999)). Of males identified to be paired in the breeding and nonbreeding seasons, 94.3 and 91.0%, respectively, were found to be members of dyads that had significantly large associations (permutation test, 10,000 permutations, SD = 0.073, n = 18 pairs). By comparison, the average COA was 0.753 (range 0.701–0.927, SD = 0.118, n = 16 pairs), although this mean increased to 0.815 if males with pair bonds that only lasted ≤4 years were removed (range 0.701–0.927, SD = 0.073, n = 11 pairs). By comparison, the average COA for two individuals associating at random in a given year was 0.012 (permutation test, 10,000 permutations, SD = 0.0021). The average minimum age of all males to form their first pair bond was 11.05 years, ranging from 6 to 19 years (n = 19 males) (Fig. 2).

Forty-three percent of males, on average, were categorized as unpaired each year; this represented 30 individual males. Of these unpaired males, 40.0% of them had previously not had a partner and their mean age (11.02 years) was similar to the mean age at which males first formed pair bonds (11.05–11.79 years). Nearly 37% of the unpaired males had a previous partner and their mean age was 23.03 years. There were insufficient data to determine whether the remaining 23.3% of unpaired males had previously had a partner. Additionally, we found that as male age increased, there was a linear increase in the proportion of paired males (linear regression, $r^2 = 0.896$, $p = 0.000$) (Fig. 3). Furthermore, as male age increased, the proportion of males that have or have had a partner also increased (logistic regression, $r^2 = 0.935$, $p = 0.000$) (Fig. 3).

The longitudinal nature of this study also afforded us the opportunity to document the ending of pair bonds due to the death of a partner. From 1980 to 2000, six pair bonds ended because one of the partners died ($n = 5$) or disappeared and was presumed dead ($n = 1$).

### Spatial patterns of association of paired and unpaired males

#### With males

To examine potential differences between paired and unpaired males in spatial patterns of association, males were categorized by their pairing status, and mean and maximum COAs were calculated for each combination of interactions between and within these male categories (Fig. 4). The mean COA is an estimate of the probability that a randomly chosen member of category $X$ was associated with a randomly chosen member of category $Y$ during any sampling period; the maximum COA between categories $X$ and $Y$ is the average of the largest COA between each member of category $X$ and any member of category $Y$ (Baird and Whitehead 2000). Annually and seasonally, mean levels of association between paired and unpaired males were zero and were the only COA values among mean and maximum values of paired and unpaired males lower than random levels of association (Fig. 4). Maximum association levels between these categories of males remained low (Fig. 4b). These data suggest the rarity of interactions between paired and unpaired males. Mean levels of association of unpaired males with other unpaired males were also low, ranging from 0.01 in the breeding season to 0.02 annually and in the nonbreeding season (Fig. 4a). Maximum levels of association within this category ranged from 0.13 to 0.18 and were similar annually and between seasons (Fig. 4b), reflecting higher levels of association among unpaired males than between paired and un-

## Table 2. Summary of the proportion of males categorized as paired and unpaired annually, 1993–2000.

<table>
<thead>
<tr>
<th>Year</th>
<th>Year</th>
<th>No. of males categorized as paired</th>
<th>No. of males categorized as unpaired</th>
<th>No. of total males</th>
<th>Proportion paired</th>
<th>Proportion unpaired</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>0.354</td>
<td>12</td>
<td>5</td>
<td>17</td>
<td>0.706</td>
<td>0.294</td>
</tr>
<tr>
<td>1994</td>
<td>0.585</td>
<td>17</td>
<td>7</td>
<td>24</td>
<td>0.708</td>
<td>0.292</td>
</tr>
<tr>
<td>1995</td>
<td>0.614</td>
<td>18</td>
<td>9</td>
<td>27</td>
<td>0.667</td>
<td>0.333</td>
</tr>
<tr>
<td>1996</td>
<td>0.630</td>
<td>16</td>
<td>13</td>
<td>29</td>
<td>0.552</td>
<td>0.448</td>
</tr>
<tr>
<td>1997</td>
<td>0.707</td>
<td>14</td>
<td>15</td>
<td>29</td>
<td>0.483</td>
<td>0.517</td>
</tr>
<tr>
<td>1998</td>
<td>0.829</td>
<td>16</td>
<td>18</td>
<td>34</td>
<td>0.471</td>
<td>0.529</td>
</tr>
<tr>
<td>1999</td>
<td>0.881</td>
<td>18</td>
<td>19</td>
<td>37</td>
<td>0.486</td>
<td>0.514</td>
</tr>
<tr>
<td>2000</td>
<td>0.750</td>
<td>16</td>
<td>17</td>
<td>33</td>
<td>0.485</td>
<td>0.515</td>
</tr>
<tr>
<td>Mean</td>
<td>0.669</td>
<td>15.9</td>
<td>12.9</td>
<td>28.8</td>
<td>0.570</td>
<td>0.430</td>
</tr>
</tbody>
</table>

Note: For 1994, there is an odd number of paired males because one member of the pair had the average minimum number of sightings, while the other member of the pair had less than the average minimum number of sightings, and therefore, was not counted.
paired males. The greatest mean and maximum COA values were found between paired males, indicative of the high levels of interaction between members of a given pair of males, and there was little difference between seasonal and annual values (mean COA = 0.03–0.04, maximum COA = 0.71–0.75) (Fig. 4). These data were based on associations between all individual males, regardless of whether they were paired or unpaired.

When considering group sightings with PG 1 or PG 2 (the criteria used for this study, see Methods section), overall, males were found in about one third of these groups, but the number of males per group varied seasonally. Of groups sighted in the breeding and nonbreeding seasons, 30.24 and 37.34%, respectively, contained at least one paired or unpaired male. Groups containing two or more males (either unpaired or from different pairs) were 1.81 times more likely to occur in the nonbreeding season than in the breeding season. Additionally, groups containing either at least two members of two different pairs of males or at least two unpaired males were nearly twice as probable in the nonbreeding season as in the breeding season. For both paired and unpaired males, only mean levels of association with FPR and FNR exceeded zero and in all cases were within an order of magnitude of random levels of association (Figs. 5a and 5b). Paired and unpaired males had identical nonzero mean levels of association with FPR and FNR in the breeding and nonbreeding seasons, respectively (Figs. 5a and 5b). The only difference in mean levels of association occurred annually with FNR; paired males had a zero level of association in this case, while for unpaired males, the value was identical to that for FNR in the nonbreeding season.

Maximum levels of association with different classes of females show similar trends in association patterns between paired and unpaired males (Figs. 5c and 5d). All values were at least one order of magnitude greater than random levels of association. The lowest maximum levels of association in all cases were with FNB. In the breeding season, for paired males, highest maximum levels of association were with FPR and for unpaired males with FUR and FPR. In the nonbreeding season, highest maximum levels of association for paired and unpaired males were with FNR.

**Temporal patterns of association of paired and unpaired males**

**With males**

LARs for paired males were high (COA = 0.6–0.7), stable over 6–7 years (Fig. 6), and differed substantially from the null model (the expected value of the LAR if there was no preferred association). These data included associations both within and between pairs of males. LARs of unpaired males were lower and declined over 5–6 years from a COA of ~0.25 to ~0.05, although at all times remaining greater than

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the null model (Fig. 6). LARs of paired males with unpaired males were extremely low and highly unstable and did not differ substantially from the null model after approximately 1 year (Fig. 6).

**With females**

For paired and unpaired males, LARs with FPR were unstable and higher in the nonbreeding than in the breeding seasons but overall showed low levels of association (all COA values <0.19 but most <0.1) (Fig. 7a). LARs with FNR showed a less well-defined pattern of association for both categories of males, but again, overall levels of association were low (COA < 0.1) and unstable; unpaired male LARs were slightly higher than those of paired males with FNR (Fig. 7b). The lowest LARs for paired and unpaired males were found with FNB, with a maximum COA of ~0.09, declining to 0.00 for both male categories after 3.5 years. LARs for unpaired males were slightly greater than those for paired males with this class of females for nearly the entire dataset. Because, by definition, a FUR is in a transitional period between FPR and FNR, and consequently spends the least time in this category, there were too few occurrences of FUR to calculate LARs with paired and unpaired males.

**Ranging patterns**

Seven male pairs and seven unpaired males met the minimum number of sightings criteria for examining ranging patterns. Within paired males, we found no significant difference ($p = 0.465$) in area between when we used sightings including both members of a pair and when we used sightings including either member of a pair. Therefore, for paired males, we examined all pairs for which there were a minimum of 100 sightings when at least one member of the pair was present, which increased our sample of the number of pairs we could analyze.

Land was removed from all area estimates because this improved both the absolute accuracy of measurements by excluding nonusable habitat and the relative accuracy of the estimates, as different males were found to have disproportionate amounts of land in their area estimates. Because ranging area estimates are biased by locational data that are autocorrelated, to test for autocorrelation for each of the unpaired males and male pairs, we calculated Schoener’s ratio ($t^2/r^2$), where $t^2$ is the mean squared distance between successive observations and $r^2$ is the mean squared distance from the center of activity (Schoener 1981; Swihart and Slade 1997). Although values of 2.000 indicate that locational data are independent of one another, Swihart and Slade (1997) showed that if $1.400 < t^2/r^2 < 2.000$, while data are moderately autocorrelated, the corresponding increase in negative bias is minimal (<5%, i.e., range areas calculated from data that are moderately autocorrelated will be less than, and within, 5% of true range areas).

Values of $t^2/r^2$ ranged from 0.806 to 1.809 for paired males ($n = 7$ pairs, mean = 1.429) and 0.999 to 1.805 for unpaired males ($n = 7$ unpaired males, mean = 1.505). Five pairs of males and five unpaired males had values of $t^2/r^2$ that were >1.400, and thus they were selected for analyses; of these males, the paired males had a combined average of 238.8 sightings per pair, and the unpaired males had an average of 159.8 sightings. Paired males had a significantly larger overall ranging area (95% UD) than unpaired males ($p = 0.000$) and also a significantly larger measure of core area at the 25% UD level ($p = 0.016$). At the 50% UD level, the difference in core area between paired and unpaired males was insignificant at $p = 0.059$ (Table 3, Fig. 8). Ranging areas defined from sighting data in censuses appeared to be representative of ranging areas defined from radio-tracking and focal observation periods. We conducted a combination of radio-tracking and focal animal observations on six of the seven pairs of males and two of the seven unpaired males.
and compared locational data collected during these efforts with the overall ranging area estimates. Across all males, 89.6% of the focal animal and radio-tracking locations occurred within the respective 95% UD values (SD = 16.2%, range 53.3–100.0%). Furthermore, when the pair for which only 53.3% of the focal animal and radio-tracking locations occurred within the 95% UD was removed (FB58 and F174), this average increased to 94.8% (SD = 7.4%, range 81.7–100.0%).

Discussion

Pair bonding is the norm

Over the 8 years of this study, 57.0% of males at least
Fig. 5. Mean levels of association (coefficient of association (COA)) of paired (a) and unpaired (b) males and maximum levels of association of paired (c) and unpaired (d) males with females of different reproductive status (nonreproductive immature females (FNB), nonreceptive adult females (FNR), potentially receptive adult females (FPR), and adult females of unknown reproductive status (FUR)), annually and seasonally. The horizontal black line indicates the level of association for two individuals associating at random during that time interval (permutation test, 10,000 permutations).
7 years old were paired in any given year and the remainder were unpaired. This suggests the existence of differing or competing male strategies. However, 7 years old is the minimum age of pair-bond formation and most bonds formed while males were in their early teens. Consequently, when these data are re-examined using this more realistic age of pair-bond formation, a different pattern emerges. Over the same 8-year time period, 84.1% of males at least 15 years old either currently have or have once had a partner and this increases to 93.8% by age 20 (Fig. 3). Additionally, 71.9% of males 20 years or older are paired annually (Fig. 3). These data combined with the finding that there is a strong relationship ($r^2 = 0.896$) between age and the proportion of males that are paired, and an even stronger relationship between age and the proportion of males that either have or have had a partner ($r^2 = 0.935$), suggest that pair bonding is the norm among adult males. The majority of unpaired males either may be too young to have yet formed a pair bond or their partner has died and they have not yet formed a new partnership. Therefore, unpaired males may be in an intermediate stage or between partners, instead of pursuing an alternative strategy.

Only one male in this study (F106) about whom we have a complete sighting history was old enough to form a pair bond and had never done so. However, he may still form a pair bond, as one male (FB32) in the study did not form his first pair bond until age 19, the same age as F106 in 2000. Two other males with complete sighting histories (F108 and FB78) are also older (age 22 and 28 in 2000, respectively) and while both have been previously paired, they have been unpaired for the majority of their adult lives. These cases could result from a combination of factors: demography may be such that few potential partners are available, these particular males may be undesirable partners for unknown reasons, or a few males may have a preference for remaining unpaired if doing so conferred a reproductive advantage. Paternity testing will allow the evaluation of this last factor. The data show that these unpaired males are the minority of all unpaired males and that for most males, not having a partner seems to be an intermediate stage rather than an alternative strategy.

Males rarely associate with nonpartner males
Overall, temporal and spatial association data showed that males generally do not associate with males other than their partners. Mean levels of association with nonpartner males for both paired and unpaired adult males in Sarasota were very low, both annually and seasonally. The highest mean values were found between paired males, but these data included associations both between and within established pairs of males (this is also the reason why maximum levels of association between paired males were so high). Consequently, mean values of association between nonpartner males that are members of different pairs (excluding mean values of association between males that are members of the same pair) would be even lower than those presented here. Similarly,
Fig. 7. LARs for paired and unpaired males with potentially receptive adult females (FPR) (a), and nonreceptive adult females (FNR) (b). LAR is an estimate of the probability that two individuals interacting (or associated) on any given day are interacting (or associating) x days later (Whitehead and Dufault 1999). Time is depicted along the x axis both annually (below) and seasonally (above) (Br, breeding season, 15 April – 30 September; Nbr, nonbreeding season, 1 October – 14 April). Bold vertical lines are approximately ±1 SE based on a jackknife procedure where data were grouped annually; dashed vertical lines indicate breaks between the breeding and nonbreeding seasons. The null association rate is the expected value of LAR if there is no preferred association. However, because each of the calculated null association rates approximates zero, they are located on top of each other along the x-axis. Both figures were based on data analyses for 1993–2000; however, LARs were only able to be calculated for 1993–1998 (a) and 1993–1999 (b) because of the overall low-level associations of adult males with adult females.
LARs for paired males were high and stable throughout the study, but again, these included associations both between and within pairs of males. As a result, because the LAR remained high, these data are more indicative of the strength and stability of the pair bond within particular pairs of males, in spite of the lack of associations between pairs of males.

Among unpaired males, mean and maximum levels of association were also low but in all cases at least one order of magnitude greater than random levels. Based on previous findings that having reached independence, males associate in groups with other males of similar ages, usually prior to pair-bond formation (Wells et al. 1987; Wells 1991), we would expect there to be low, nonrandom levels of association between unpaired males. Furthermore, our ability to document the initiation of a pair bond necessarily occurs some brief time following actual pair-bond formation because we detect pair-bond formation as a change in association patterns over a period of time. Consequently, following actual pair-bond formation, but prior to being categorized as paired males, some males may be erroneously documented as unpaired, leading to higher mean values of association between all unpaired males. These factors also explain the moderately low LAR between unpaired males, which declined as the time lag between observations increased over the course of the study.

Between paired and unpaired males, both the spatial and temporal association data show extremely low and unstable patterns of association. Thus, from these data, it is clear that adult males rarely associate with nonpartner males. This is in sharp contrast with a study of male alliances among dolphins in Shark Bay, Australia, which showed not only that there is cooperation within male alliances but also that pairs of alliances will act together to aggressively capture a female from another alliance of males (Connor et al. 1992). Our data do not support the presence of such second-order alliances in Sarasota Bay bottlenose dolphins. Adult males are rarely found in groups with males other than their partners. However, multimale groups containing nonpartner males (both paired and unpaired) were nearly twice as frequent in the nonbreeding season, and this could not be attributed to seasonal differences in group size. This was also reflected in the spatial patterns of association by a slight increase from the breeding to the nonbreeding season in the mean COA among both unpaired and paired males.

As a result of intersexual differences in rates of reproduction, among mammals, males are predicted to be the “competitive” sex and females the “choosy” sex (Clutton-Brock and Vincent 1991). Thus, in this context, it is interesting that in the Sarasota community, there is not more direct interaction among nonpartner adult male dolphins. Intrasexual competition should be most intense during the breeding season, especially when there are a limited number of potential mates, as is the case in bottlenose dolphins where females are asynchronous breeders and the interbirth interval is on average 3–6 years (Wells and Scott 1999). The lack of association between nonpartner males suggests that the costs of interacting with males other than alliance members are substantial, and these costs may be partially reduced in the nonbreeding season when competition for mates is reduced.

Because of the cost of aggressive interactions among males, nonpartner males may seldom interact. Bottlenose dolphins in Sarasota are moderately sexually dimorphic, with some of the more pronounced intersexual differences being found in potential weapons and modes of propulsion (Tolley et al. 1995), suggesting the importance of intrasexual competition among conspecifics. In addition to their increased size, males are much more likely than females to have white scarring on their dorsal fins, indicative of aggressive interactions between individuals (Tolley et al. 1995). The cost of aggressive exchanges may be such that rather than risking a potentially debilitating interaction, it may be a better strategy to avoid such interactions, particularly when costs are greatest (in the breeding season). Additionally, if any dominance relationships among nonpartner males exist, as have been observed in captive settings (Ostman 1991; Samuels and Gifford 1997), this may also affect the decision to interact with particular males. To date, there is no evidence for such dominance relations, but current detailed behavioral studies should elucidate this possibility.

**Males preferentially associate with females with the greatest reproductive potential**

Overall, the spatial-association data show no significant differences annually and seasonally between paired and unpaired males in levels of association with females regardless of reproductive state. All mean levels of association were extremely low and were within an order of magnitude of random levels of association, but still higher. Despite being low, these data show that all males preferentially associated with FPR during the breeding season and with FNR in the nonbreeding season. Maximum levels of association show a similar trend and in all cases were more than one order of magnitude greater than random levels of association. During the breeding season, paired males had their highest maximum levels of association with FPR, and for unpaired males, their highest maximum levels of association during this season were with FUR and FPR. Males had highest maximum levels of association with FNR in the nonbreeding season, and
at all times, annually and seasonally, maximum levels of association were lowest with FNB. These data follow the expected trend of males associating more frequently with adult females than immature females, and in the breeding season, of interacting most often with females that are potentially receptive. This supports previous work in Sarasota which demonstrated that in the breeding season, mature males are significantly more likely to be sighted with receptive females than with nonreceptive females (Moors 1997). A similar but much more striking pattern was found in studies in Shark Bay where adult male alliances are more likely to herd, and have higher associations with, females during the years in which they are cycling than in the years in which they are pregnant (Connor et al. 1992a; Smolker et al. 1992).

LARs for paired and unpaired males lend support to the spatial-association data for FPR, FNR, and FNB. Overall, the temporal measures of association (LARs) are of greater magnitude than the spatial measures of association, which implies that repeated interactions of specific pairs of males and females do occur, although most male–female associations are infrequent, leading to the overall instability of the LARs. LARs of males with adult females suggest seasonal patterns of association, although this pattern is strongest and most evident with FPR. LARs with FPR are more stable and considerably greater in the nonbreeding season than in the breeding season for both paired and unpaired males. This may result from several factors. Males may form associations with females prior to their receptive periods because it may be more difficult to form such an association once a female is more attractive and male–male competition increases, as has been previously suggested for chimpanzees (Pan troglodytes) and bottlenose dolphins (Goodall 1986; Connor et al. 1996; Moors 1997). However, because the increase in LAR occurs in the middle of the nonbreeding season rather than immediately prior to the breeding season, this explanation is not completely satisfactory. Alternatively, owing to intense male–male competition during the breeding season, males may associate with females in the nonbreeding season if such associations create affiliative relationships that confer a future advantage through increased mating opportunities. It has been suggested that the formation of a strong bond between male and female baboons (Papio cynocephalus) may boost a male’s future mating success in two ways: (1) an affiliative bond may have a positive effect on the female’s cooperation during subsequent receptive periods and (2) a conflict over a female among males can be decided to the advantage of the male with the stronger bond (Noë and Sluijter 1990). Furthermore, such associations outside of the breeding season may provide females with the opportunity to evaluate males (Connor et al. 1996; Moors 1997) and may also be a mechanism to reduce the risk of infanticide by allowing females access to more males overall within a given year (Connor et al. 1996).

In agreement with the spatial patterns of association, the lowest LARs of paired and unpaired males are with FNB, which is in accord with males focusing their efforts on adult females. These LARs are also the least stable, showing a steady decline to zero after 2.5–3.5 years for both paired and unpaired males. This decline is an artifact of the definition of FNB, which include independent females <5 years old. Calves remain with their mothers for 3–6 years, but some have become independent as young as age 2 (Wells and Scott 1999). Consequently, for these analyses, the longest possible duration of association of a male with a nonreproductive female was ~3 years, but most females were only in this category for 1 year. This leads to the decline in LARs as FNB enter the cohort of potential breeding females.

In summary, male patterns of association with females, although more subtle than in other studies, are in accordance with predictions that males should associate most strongly with those females having the greatest reproductive potential. These associations with adult females are unstable, but repeated interactions between specific male–female pairs do occur. Additionally, the nonbreeding season may also be an important period for males to establish relationships with females that may confer future reproductive benefits. More fine-scale behavioral observations of paired and unpaired males in the breeding and nonbreeding seasons (currently being conducted) are needed to further elucidate these interactions and may reveal patterns not obvious at the grosser scale of these analyses.

**Comparing association patterns of paired and unpaired males**

Both spatial and temporal measures of association indicate no substantial differences in patterns of association between paired and unpaired males with females of differing reproductive states. This may result from patterns of association that have become entrenched throughout the adult years of an individual. Most adult males are paired for a substantial portion of their adult lives. Consequently, in the absence of a partner, male patterns of association may not be greatly altered because males may simply continue to follow the same patterns established when they were pair bonded.

This lack of a difference between paired and unpaired males in their patterns of association with females does not exclude, however, one of the hypothesized functions of the pair bond: increased access to females (Wells 1991; Connor et al. 1992a, 1992b). The data used in this study are based on group membership, which is an instantaneous “snapshot”. Paired males may be able to maintain exclusive access to a female over longer periods of time than unpaired males, including guarding her during non-daylight hours, they may be more effective in continuing to maintain access to a female in the presence of other males, and they may be more capable than unpaired males of capturing a female from a group of females or from a consortship with other males. None of these parameters are represented in the methods of the current study.

**Sighting data accurately represent male ranging patterns**

The comparison of the overall ranging area calculated using sighting records from standardized surveys with geographic locations collected during both focal animal observation periods and radio-tracking efforts suggest that in general the calculated area estimates and geographic ranges are representative of the habitat that these individuals use. Based on this comparative technique, the 95% UD failed to accurately represent area usage for only one of the eight male units examined; members of this pair have been previously observed to range well outside the Sarasota survey effort region. For
Fig. 8. Core areas calculated as the 25% UD (a) and 50% UD (b) for males that had a minimum of 100 sightings and maintained the same male category status (paired or unpaired) throughout the period 1993–2000. Individual animal codes are FBXX or FXXX where F or FB stands for "freeze-brand", a means of unambiguously identifying by number each dolphin handled and sampled.
the remaining males, however, on average, 94.8% of the locations recorded during focal animal observation periods or radio-tracking efforts occurred within the 95% UD for these males. This supports the notion that the calculated area estimates and range locations using the fixed-kernel method are representative of actual ranging patterns of individuals within this community despite inherent survey effort biases.

Mean values of Schoener’s ratio for all paired and unpaired males indicated that the locational data were at worst moderately autocorrelated. Swihart and Slade (1997) found that as levels of autocorrelation increased (smaller values of \( r^2 \)), negative bias in home-range estimators increased, i.e., as autocorrelation increased, calculated ranging area estimates were increasingly smaller than true ranging areas. However, they found that the level of this increase in negative bias was minor (<5%) for moderate levels of autocorrelation (1.400 < \( r^2 < 2.000 \)), and even when \( r^2 = 1.000 \), the increase in negative bias was <10% (Swihart and Slade 1997). Because we selected only those males with \( r^2 < 1.400 \), calculated estimates of overall ranging area and core area are reliable and observed differences between the two categories of males are valid.

Comparing ranging patterns of paired and unpaired males

Paired males had a significantly larger overall ranging area than unpaired males. This supports one of the hypothesized advantages of pair bonding (Wells 1991). Once a male forms a pair bond, as a member of a pair, that male is able to range farther, perhaps owing to increased vigilance and protection from predators and potentially threatening conspecifics. This increase in ranging area may allow paired males to encounter more females (Wells 1991). To date, paired males have been observed farther outside the Sarasota community range than unpaired males and sometimes in association with females in these adjacent communities. Paternity analyses show that more than 40% of calves born in the Sarasota community are sired by males from neighboring communities (Duffield and Wells 2002; Wells 2003; Wells et al. 2001), and thus it is likely that paired males, having larger ranges and being able to travel farther into neighboring communities, increase their mating opportunities.

Paired males were also found to have significantly larger core areas at the 25% UD level, and at the 50% UD level, this same trend was apparent although not significant (\( p = 0.059 \)). This lends further support to one of the hypothesized advantages of pair bonding, as discussed above, of paired males having larger ranges than unpaired males. Additionally, when qualitatively examining core areas for males that maintained the same status (paired or unpaired) for the duration of this study, core areas were found to form a patchwork mosaic throughout the study area with considerable overlap among them (see Fig. 8). These data support the idea that adult males are not territorial within the range of the community, although occasional violent interactions along community borders leave the question of defended areas unresolved (Wells 2003). Furthermore, this overlap in core areas would be predicted to increase the occurrence of interactions between nonpartner males. However, in light of the finding that such interactions are rarely observed either during surveys (see above) or during focal animal observation periods (E.C.G. Owen, personal communication), this further suggests that males actively avoid interactions with males other than their partners, particularly in the breeding season.

Evidence for alternative male strategies?

In summary, association and ranging data provide scant support for paired and unpaired males existing as alternative strategies. While there are clearly two different conditions for adult males in the Sarasota community, paired or unpaired, no evidence was found from the parameters analyzed in this study (association and ranging patterns) to suggest that paired and unpaired males are employing different tactics, a requirement of condition-dependent strategies (Gross 1996). The majority of males in Sarasota waters form pair bonds, and lack of a partner appears to be an intermediate or transitional state. This likely contributes to the lack of substantial differences between association patterns of paired and unpaired males with females of different reproductive states. While results of a paternity study currently underway will ultimately determine the existence of alternative strategies in this system, data from this study suggest pair bonding as the prevalent male strategy and that previous work in Sarasota Bay (Wells et al. 1987; Wells 1991) identified resultant patterns rather than indications of possible strategies.

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