Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence

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Bottlenose dolphin (*Tursiops* sp.) calves are unusual among social mammals in that they have a have prolonged nursing period (3—8 years), but precocious motor ability, enabling them to separate from their mothers and form distinct social bonds at an early age. We examined two measures of calf sociality from birth to 4 years of age: (1) the number of unique associates and (2) the proportion of time that calves spent in groups with nonmothers. Calves ($N = 89$) associated with a mean $\pm$ SE of 27.56 ± 2.24 individuals (range 0—77) and spent $46.84 \pm 3.00\%$ of their time in groups (range 0—100%). Mothers ($N = 49$) averaged 39.39 ± 5.32 associates (range 0—139), when data were combined across all years (and often multiple offspring). Both calf characteristics (sex, age and separation time) and maternal characteristics (sociality and foraging time) contributed to this variation. Although calf associate number and time in groups were positively correlated, sex and age-specific patterns differed depending on the measure used. As separation time increased, both sexes increased associate number, but females decreased and males increased time in groups, indicating that males sought more social contact. Maternal socioecological strategy largely contributed to calf social development, particularly for daughters. As maternal foraging time increased, maternal and calf sociality decreased. Second, the number of associates that calves had when with their mothers predicted associate number during separations, but time spent in groups was not similarly correlated. These early patterns probably influence subsequent social development, including the structure of female networks and male alliances.

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A range of mammalian studies show relationships among relative brain size, social complexity and life history traits (Harvey & Clutton-Brock 1985; Sawaguchi 1990; Sawaguchi & Kudo 1990; Dunbar 1992; Gittleman 1994; Barton 1996; Marino 1996, 1998; Joffe 1997; Kudo & Dunbar 2001; Deaner et al. 2003; Ross 2003; Byrne & Corp 2004; Leigh 2004; Schultz & Dunbar 2006). Presumably, socially complex mammals (i.e. those that form long-term, individually specific bonds) would face sex-specific selection pressures to become socially adept by reproductive age. Prolonged immaturity may enable individuals to acquire the skills necessary to negotiate

demanding social and ecological environments while still under the protection of their mothers (Byrne & Whiten 1988; Pagel & Harvey 1993; Joffe 1997). Sex differences in juvenile behaviour foreshadow differences in adult behaviour and social organization in many mammals (e.g. primates: Meaney et al. 1985; van Noordwijk et al. 1993; Watts & Pusey 1993; ungulates: Pratt & Anderson 1979; Berger 1980; Byers 1980, 1984; Lee 1986; Mathisen et al. 2003; canids: Holekamp & Smale 1998; delphinids: Mann 2006). Fewer studies have found sex differences in behaviour preweaning (exceptions see: primates: Berman 1982; Förster & Cords 2005; Lonsdorf 2005; ungulates: Pratt & Anderson 1979; Lee 1986; delphinids: Scott et al. 2005; Mann 2006).

Unlike other species with slow life histories that remain in their natal group during the juvenile period (e.g. primates: Leigh & Blomquist 2007; elephants: Moss

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2001; some toothed whales: Whitehead & Mann 2000), bottlenose dolphins (*Tursiops* sp.) markedly reduce association with their mothers at weaning (Mann et al. 2000), but develop and maintain long-term bonds within a fluid, fission–fusion social system (reviewed in Connor et al. 2000). Thus, social organization is likely to shape the timing (e.g. pre- versus postweaning) and nature of learning and maturation. For example, mammals in stable groups or that maintain kin associations postweaning would be buffered or protected from costly social and ecological (e.g. foraging and predation) mistakes. In contrast, if mother–offspring association drops significantly at weaning, offspring competence must be achieved relatively early. We suggest that bottlenose dolphins, compared to most taxa with similarly slow life histories, must learn to navigate their social and physical environments by the end of infancy (typically 3–6 years, from birth through weaning), despite a prolonged juvenile period (>8 years, from weaning to reproductive maturity; Mann et al. 2000). In the 2-year postweaning, bottlenose dolphin mother–offspring association averages 25.3% of the time (Mann et al. 2000). Previous studies of *Tursiops* in Shark Bay, Australia have focused on calf foraging development (Mann & Sargeant 2003), association and factors related to calf mortality (Mann et al. 2000; Mann & Watson-Capps 2005). Here, we examine the emergence of social skills in wild bottlenose dolphin calves by identifying factors (calf sex, age and maternal behaviour) that contribute to individual variation in sociality.

Despite the attention that has been given to the complex nature of fission–fusion society in bottlenose dolphins (e.g. Connor et al. 1998, 2000, 2001; Lusseau 2003; Wells 2003; Lusseau & Newman 2004), the role of early experience in social development has not been explored. Although variation in female sociality is considerable (Smolker et al. 1992) and is likely to impose constraints upon calf social development, physically precocious calves have social options independent of their mothers (Mann & Smuts 1999). Dolphin calves appear to emulate the adult social structure by joining and leaving their mothers from an early age, typically to forage or socialize (Mann & Watson-Capps 2005). These temporary separations are frequent and often long-distance; even newborns, 0–3 months old, have been observed greater than 100 m from their mothers (Mann & Smuts 1999). During separations from their mothers, calves may be alone (solitary separation) or with others (social separation) either from within or outside of their mothers' network of close associates (Mann & Smuts 1998). This pattern, which is rare among mammals with long periods of dependency, provides us with the unusual opportunity to investigate the effect of maternal presence on the development of association patterns in calves from birth to weaning.

Social development in bottlenose dolphins occurs within a sex-segregated society, reflecting the different reproductive strategies of males and females (Wells et al. 1987; Smolker et al. 1992; Connor et al. 2000, 2006). Adult males form alliances with other males in which they cooperate to obtain and sequester, often through the use of aggression, an individual cycling female (Connor et al. 1992). At several study sites, males form first-order alliances in which they pair with one or two other males

(Owen et al. 2002; Parsons et al. 2003). But in Shark Bay, males form hierarchical multilevel alliances of 2–14 dolphins (i.e. teams of first-order alliances; Connor et al. 1992, 1999). In contrast, adult females form loose social networks with other females of varying age (Wells et al. 1987; Smolker et al. 1992), often including matrilineal kin (Möller et al. 2006). Variation in female sociality is likely to be primarily driven by prey distribution, habitat heterogeneity and foraging tactics, which vary widely between individual females (Mann & Sargeant 2003; Sargeant et al. 2005, 2007). Because foraging is a predominantly solitary activity, females that specialize in foraging types that require a relatively high time investment (e.g. sponge-carriers, Mann & Sargeant 2003) have few opportunities to associate with others. Thus, adult females may range along a continuum from highly social with low foraging demands to predominantly solitary with high foraging demands.

This variation in maternal socioecological strategy is likely to affect the social development of male and female calves differently. Although both sexes show natal philopatry (Connor et al. 2000), daughters associate more with their mothers after weaning than do sons (Samuels 1996) and appear to develop foraging tactics similar to their mothers (Mann & Sargeant 2003). In contrast, males are reported to associate in fluid, highly sociable, and predominantly male, groups of juveniles after weaning (Sarasota, Florida: Wells et al. 1987; Wells 1991), and form alliances as they approach sexual maturity in their early teens (Sarasota, Florida: Owen et al. 2002). Thus, calves are likely to face sex-specific social (and ecological) challenges prior to weaning. Males are likely to be attracted to potential alliance partners and begin developing strong male–male bonds. Females are likely to develop social and foraging patterns similar to their mothers. Since the sociality of mothers dictates, in part, the social experiences available to calves, maternal sociality can influence the type of alliances (e.g. stable versus labile first order) eventually formed by sons and/or the socioecological strategies of daughters. By comparing association patterns of calves when calves were with and separated from their mothers, we can determine how maternal social patterns differentially affect daughters and sons early in development.

We assessed the social patterns of mothers and calves using two measures of sociality: (1) the number of associates, which measures how many unique dolphins that the mother and calf encounter and potentially form relationships with; (2) the proportion of time in groups (i.e. in association with others besides the mother), which indicates allocation of time to social contact or stimulation. Both measures have implications for social cognition (see Joffe & Dunbar 1997). Although slightly different, we expected these measures to be positively correlated. To determine the extent of maternal influence, we used both measures to compare calf sociality when calves were with and separated from their mother. If maternal sociality influenced the calf, then calf social patterns when with and away from the mother would be positively correlated. Similarly, sex differences in sociality were predicted to emerge pre-weaning in bottlenose dolphins and reflect sex-specific reproductive and socioecological strategies of adulthood.

Mothers are likely to determine social patterns (who to join and leave) most of the time, but when the calf is separated, we expected sex differences to be most apparent and to strengthen with age as calves neared independence. Specifically, male calves were predicted to engage in more (percentage of time) social separations and to have more associates during separations than female calves. Female calves were predicted to mirror maternal social patterns more than male offspring. To facilitate interpretation of differences in sociality, we also analysed calf activity.

METHODS

Study Site, Subjects and Data Collection

Our study site encompasses an area of approximately 250 km^2 offshore of Monkey Mia in Shark Bay, Western Australia (25°47′S, 113°43′E). Shark Bay, site of the second-longest running dolphin project worldwide, is exceptional for studies of cetacean social development because behaviours are easy to observe in the shallow, clear water and individual life histories are well known. The study population includes over 1200 individually recognized bottlenose dolphins (*Tursiops* sp.) sighted since 1984. Shark Bay bottlenose dolphin mothers ($N = 49$) and calves ($N = 89$) have been studied annually since 1988 (Mann & Watson-Capps 2005). During boat-based focal follows (Mann 1999) on specific mother–calf pairs, detailed behavioural information (e.g. group composition, activity, mother–calf proximity, social interactions, etc.) was collected using a combination of point and continuous sampling techniques (Altmann 1974). Association was conservatively determined via a 10 m chain rule (Smolker et al. 1992) in which a dolphin was considered to be in the group if it was within 10 m of another dolphin in the group. Temporary mother–calf separations were defined as when the calf was more than 10 m from the mother and no other dolphins were linking them by 10 m. During temporary mother–calf separations, we typically stayed with the calf but continued data collection on the mother whenever possible.

Our analyses include focal data for calves, from birth through weaning, collected during 1989–2006, but exclude data on calves older than 4 years because most calves are weaned by age 4 (Mann et al. 2000) and because our sample size was limited for older calves. For calves weaned prior to age 4, postweaning data were excluded. Only calves that were observed more than 1 h in at least one age class were included in analyses. These criteria generated a total of 1165.3 h of focal calf data (1157.9 h for mothers). Observation time ranged from 1.0 to 50.7 h ($\overline{X} \pm SE = 13.09 \pm 1.27$; $N = 89$) per calf and 1.0 to 91.7 h ($\overline{X} \pm SE = 23.63 \pm 3.60$; $N = 49$) per mother. The number of calves observed per mother ranged from one to five, with a median of one calf per mother ($\overline{X} = 1.82$).

Sex and Age Determination

Throughout our analyses, data are subgrouped according to the sex and age class of the focal calf at the time of observation. Calf sex was determined primarily by opportunistic views of the genital region and, in a few cases, by DNA (Krützen et al. 2004). The sex breakdown for the 89 calves in our study was 31 female, 31 male and 27 of unknown sex.

Unless the exact birthdate of a calf was known, we estimated age based on physical and behavioural characteristics such as the presence of fetal folds or lines, surfacing behaviour and body size in relation to the mother. Young of the year, seen between 4 and 11 months of age when newborn traits had vanished, were assigned a default birthdate of 1 November, when births peak (Mann et al. 2000). Birthdates were then used to assign calves to age classes delineated in Table 1. All birthdates in this study were accurate within 6 months, but most estimates were accurate within weeks. In no instance could age class have been misassigned. Weaning age was determined by taking the midpoint between the time that a calf was last seen either swimming in infant position (in contact underneath the mother) or spending more than 80% of the time with the mother and when the mother–calf association decreased to less than 50% in our sighting records (Mann et al. 2000).

Calf Activity Budgets

The activity of the focal calf was recorded every min (post-1997), every 2.5 min (pre-1997) or for each discrete dive cycle (pre-1997). Previous comparisons of data from focal individual point samples and predominant activity samples indicated that the results from these methods are nearly identical (see Mann 1999). Thus, for calves that were followed using more than one method, data were weighted by the minutes observed with that method. Calf activities were collapsed into six categories: foraging, socializing, travelling, resting, infant position, and other (defined in Table 2).

Activity data during separations were coded as a function of mother–calf distance rather than group membership. When mothers and calves were greater than 10 m apart, they were considered separated, regardless of whether or not other dolphins were between them. This distance was selected because a mother and calf are unlikely to jointly participate in any activity if separated by 10 m or more. Using this method, a calf could be separated from its mother, but technically in the same group (defined by the 10 m chain rule) if dolphins were spread out. However, these two methods of determining separation from the mother (>10 m separation versus 10 m chain rule) are highly correlated (Spearman rank

Table 1. Calf age class definitions

Age class	Calf age (months)
0	0–2.99
1	3–11.99
2	12–23.99
3	24–35.99
4	36–47.99

Table 2. Ethogram (reproduced from Mann & Watson-Capps 2005)

Activity	Definition
Foraging	Fast swimming, rapid direction changes, bottom-grubbing, fish catches and fish fleeing
Socializing	Rubbing, petting (flipper or flukes actively moving on a body part of another), displays, chasing, mounting, poking, contact swimming (excluding infant position) and other forms of active contact
Travelling	Steady, moderate or fast (>3 k/h) directional movement. Speeds were often tracked by boat speed
Resting	Slow (<3 k/h) nondirectional movement, frequent hanging at the surface
Infant position	Calf swims under mother, in intermittent contact, with the calf's head touching the mother's abdomen

Activity categories are mutually exclusive. Infant position was recorded for calves only.

correlation: $r_S = 0.95$, $N = 87$, $P < 0.001$). The average percentage of time that calves spent more than 10 m from their mothers ($\overline{X} \pm SE = 17.74 \pm 1.48\%$, $N = 87$) and the average percentage of time that calves spent separated from their mothers using the 10 m chain rule ($\overline{X} \pm SE = 16.53 \pm 1.63\%$, $N = 89$) differed by less than 2%. Sample sizes differ because calf activity was not recorded for two calves and thus they are not included in the activity budget data set.

Statistical analyses

We examined calf activity budgets combined across age classes 0–4 and mother–calf association categories ('together with mother' and 'separated from mother'). Separate repeated measures ANOVAs (SAS v. 9.1, Proc Mixed, SAS Institute, Cary, NC, U.S.A.) were then conducted for the two activities most closely linked to sociality: foraging and socializing. The dependent variable was the proportion of time that calves spent either foraging or socializing. Independent variables included calf sex, calf age class, and whether a mother and calf were 'together' or 'separated'. Age class 0 was excluded from these analyses because only four newborns were observed separated from their mothers. These two analyses were conducted using complete third-order models (i.e. all possible two-way and three-way interactions were included) and both analyses required arcsine transformation of the dependent variable to achieve normality. To correct for heterogeneity of variance in the foraging model, variance was partitioned into two groups according to whether a mother and calf were together or separated. In the socializing model, variance was partitioned according to calf age class. Goodness-of-fit statistics (-2LL and AICC for fixed effects) were used to assess variance groupings and also to determine whether linear, log or quadratic versions of each independent variable resulted in the best model fit. The data were modelled to account for correlations between (1) calves within mother (if a mother had multiple calves), (2) age classes within calf (repeated measures), and (3) categories of 'together with mother' and 'separated from mother' within age class and within

calf. Because these models contained no continuous variables, nonsignificant interactions were not removed from the final models.

Two Measures of Sociality

We examined the variability in two measures of calf sociality: (1) the number of associates and (2) the proportion of time spent in groups with individuals besides the mother. We excluded associates whose identity was unknown (2.5% of all data points) from calculations, thus providing a conservative measure of the number of associates. The number of calf associates is presented as raw values, unadjusted for hours observed, to show the high degree of individual variation. However, we controlled for variation in observation time in our analyses. Our second measure was already adjusted for hours observed since it was calculated by dividing the number of minutes that a calf was observed in a group, with at least one other dolphin besides the mother, by the total number of minutes that calf was observed.

Statistical analyses

To examine predictors of calf sociality, we conducted five separate analyses using general linear mixed models (SAS v. 9.1, Proc Mixed) that accounted for potential correlations between calves with the same mother, as well as between different age classes for an individual calf (i.e. repeated measures design). For each measure of sociality, a separate analysis was conducted for two conditions, when calves were with their mothers (maternally driven social patterns) and when calves were separated from their mothers (calf-driven social patterns). We did not assume that maternal and calf sociality are independent, but we tested this separately by examining the relationship between calf age, sex and maternal grouping patterns, and between calf social patterns when calves were with and separated from the mother. Our sample size for analyses of calf sociality during separations ($N = 74$: 30 female, 24 male and 20 unknown sex) differs from that when calves were with their mothers ($N = 89$) because not all calves were observed separated from their mothers.

For the model examining calf associate number when 'together with mother' (the dependent variable), independent variables included calf sex, calf age class, maternal foraging time and the number of hours that a calf was observed. Maternal foraging time was included as a potential predictor of calf sociality because foraging is a predominantly solitary activity, consequently affecting calf sociality. For the model examining calf associate number during separations (dependent variable), we included the independent variables listed above and the percentage of time that calves were separated from their mothers (a measure of calf independence) and calf associate number when 'together with mother' (as a proxy for maternal sociality).

A third, separate analysis was conducted to examine calf associate number combined across all age classes and including both categories 'together with mother' and 'separated from mother'. A calf's total number of

associates is not additive across years because calves may associate with different individuals in each age class or continue to associate with the same individuals each year (e.g. a calf that has five associates in age class 1 and five associates in age class 2 may have 5–10 individual associates). Thus, one purpose of this analysis was to examine the total number of unique associates that a calf encounters during infancy. For this model, the dependent variable was a calf's total associate number (combined across age classes 0–4 and including both categories 'together with mother' and 'separated from mother'). Independent variables included calf sex, maternal foraging time, a calf's percentage of time in groups and the number of hours that a calf was observed. The percentage of time that calves spent in groups (our other measure of sociality) was included in the model to determine whether there was a relationship between these two measures of sociality. Although calves with more associates might spend more time in association with others, this is not necessarily the case. For example, a relatively solitary mother–calf pair might spend a small amount of time in very large groups. Conversely, a sociable mother–calf pair might spend a substantial amount of time with a small number of associates.

For the model examining the percentage of time that calves spent in groups when 'together with mother' (the dependent variable), independent variables included calf sex, calf age class, maternal foraging time and the number of hours that a calf was observed. For the model examining the percentage of time spent in groups when 'separated from mother' (the dependent variable), independent variables included the percentage of time separated and the percentage of time in groups when 'together with mother', in addition to the independent variables presented for the previous model.

All analyses were first conducted using complete second-order models, with all possible two-way interactions included, and normality and homogeneity of variance were graphically assessed. Two analyses of calf associate number, 'together with mother' and 'separated from mother', required log transformation of the dependent variable to achieve normality. The model for calf associate number 'together with mother' also required variance groupings, constructed according to calf sex, to correct for heterogeneous variances. Continuous independent variables were then assessed for linearity, and log transformed if necessary, to improve model fit (evaluated via corrected Akaike information criterion, AICC, statistics; SAS v. 9.1). Final models were obtained by using the backward stepwise procedure (Hendrix et al. 1982) to remove nonsignificant $(P > 0.20)$ interactions containing continuous variables, with least significant terms removed first. Our criterion for model removal was selected to maintain consistency with previous studies (e.g. Mann & Watson-Capps 2005). Class by class variable interactions and main effects for continuous variables were not removed. In analyses in which continuous variables (e.g. maternal foraging time, calf percentage of time separated) were significant $(P \leq 0.05)$ or only marginally nonsignificant $(P \leq 0.10)$, we examined the effects at low $(\overline{X} - 1\,\text{SD})$, moderate $(\overline{X})$ and high $(\overline{X} + 1\,\text{SD})$ levels of these factors. Estimate

statements (SAS v. 9.1) were then used to obtain slopes and intercepts for partial regression equations and to conduct tests of hypotheses. Pairwise means comparisons were conducted only for ANOVA effects with P values below 0.10 to limit an inflation of error rate. Age class 0 was excluded from pairwise comparisons because only six of 10 calves that were observed in age class 0 were also observed in another age class.

Observation time

Observation time was highly correlated with the number of associates. This relationship became nonsignificant at 10 h of observation per calf (Spearman rank correlation: 9 h observed, $r_S = 0.31$, $N = 42$, $P = 0.04$; 10 h observed, $r_S = 0.23$, $N = 42$, $P = 0.15$). For mothers, associate number and hours observed was weakly correlated up to 16 h of observation per mother (Spearman rank correlation: 16 h observed, $r_S = 0.37$, $N = 23$, $P = 0.08$). Because of this relationship, we treated observation time as a covariate, thereby adjusting for it in our analyses by holding it constant at its mean (6.13 h per age class, 13.09 h for all ages) in pairwise means comparisons and regression equations. The percentage of time spent in groups was not correlated with observation time for mothers or calves (Spearman rank correlation: mothers, $r_S = 0.09$, $N = 49$, $P = 0.52$; calves, $r_S = 0.03$, $N = 89$, $P = 0.76$).

RESULTS

Summary Statistics

The number of maternal associates ranged from 0 to 139 individuals (unadjusted for hours of observation; $\overline{X} \pm \text{SE} = 39.39 \pm 5.32$, $N = 49$) when data were combined across all years (including those with different dependent calves). The total number of unique calf associates ranged from 0 to 77 during the first 4 years of life (unadjusted for hours of observation; $\overline{X} \pm \text{SE} = 27.56 \pm 2.24$, $N = 89$). During temporary separations, the number of calf associates ranged from 0 to 34 (unadjusted for hours of observation; $\overline{X} \pm \text{SE} = 10.66 \pm 1.11$; $N = 82$). Similar variability was found in the percentage of time that mothers (range 0–100; $\overline{X} \pm \text{SE} = 44.91 \pm 4.34$; $N = 49$) and calves (range 0–100; $\overline{X} \pm \text{SE} = 46.84 \pm 3.00$; $N = 89$) spent in groups.

Averaged across all age classes, calves spent $16.53 \pm 1.63\%$ (range 0.0–71.4%, $N = 89$) of their time separated from their mothers. The mean proportion of time that calves spent separated from their mothers was low during the newborn period, but high at older ages (age class 0, $\overline{X} = 3.08 \pm 1.27\%$, $N = 10$; age class 1, $\overline{X} = 14.89 \pm 1.71\%$, $N = 59$; age class 2, $\overline{X} = 18.56 \pm 2.35\%$, $N = 49$; age class 3, $\overline{X} = 19.12 \pm 2.38\%$, $N = 45$; age class 4, $\overline{X} = 22.02 \pm 3.72\%$, $N = 27$). Maternal foraging time ranged from 0.0 to 76.02% ($\overline{X} \pm \text{SE} = 33.05 \pm 0.02$; $N = 89$).

Calf Activity

Calves were most frequently observed swimming in infant position with their mothers ($\overline{X} \pm \text{SE} = 39.36 \pm 1.20\%$) or resting ($\overline{X} \pm \text{SE} = 32.97 \pm 1.21\%$). Foraging

$(\overline{X} \pm \mathrm{SE} = 11.03 \pm 1.04\%)$, travelling $(\overline{X} \pm \mathrm{SE} = 8.97 \pm 0.68\%)$ and socializing $(\overline{X} \pm \mathrm{SE} = 7.21 \pm 0.81\%)$ occurred less often. Calves also spent a small amount of time $(\overline{X} \pm \mathrm{SE} = 0.46 \pm 0.08\%)$ engaged in activities that did not fit into any of the above categories (e.g. bow-riding and weed rubbing).
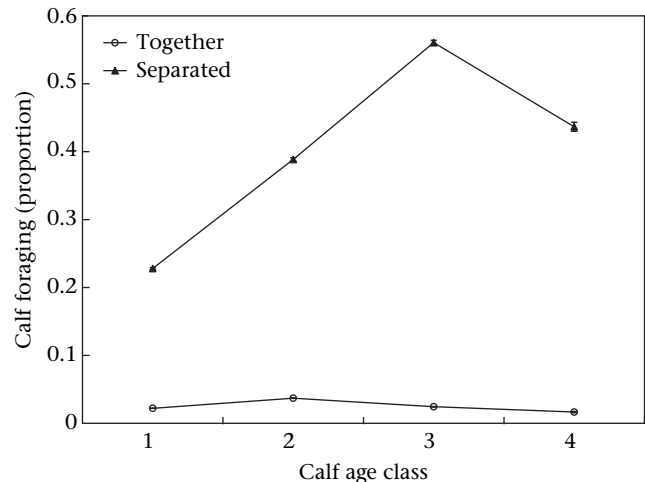
Foraging

Our analysis of variance indicated that the proportion of time that calves spent foraging was related to the interaction between calf age and maternal presence–absence (Table 3). For all age classes (1–4), calves spent a greater proportion of time foraging while separated from their mothers than while with them (paired t tests: age class 1, $t_{162} = 10.00$, $P < 0.0001$; age class 2, $t_{162} = 10.31$, $P < 0.0001$; age class 3, $t_{162} = 12.92$, $P < 0.0001$; age class 4, $t_{162} = 7.85$, $P < 0.0001$; Fig. 1). When calves were with their mothers, foraging rates were consistently low (Fig. 1); there were no differences in the proportion of time spent foraging among age classes 1–4. However, during separations from the mother, calves foraged least often in age class 1 and generally increased foraging time with age (paired t tests: age class 1 versus 2, $t_{210} = -2.81$, $P = 0.0055$; age class 1 versus 3, $t_{209} = -5.10$, $P < 0.0001$; age class 1 versus 4, $t_{215} = -2.50$, $P = 0.0133$; age class 2 versus 3, $t_{207} = -2.29$, $P = 0.0232$; Fig. 1).

Social interactions

The ANOVA for calf socializing indicated that sex and age class were significant factors (Table 3). Both sexes decreased the proportion of time spent socializing with age (paired t tests: age class 1 versus 3, $t_{111} = 2.95$, $P = 0.0039$; age class 1 versus 4, $t_{224} = 4.10$, $P = 0.0001$; age class 2 versus 4, $t_{241} = 3.19$, $P = 0.0016$; age class 3 versus 4, $t_{187} = 2.12$, $P = 0.0352$; Fig. 2). Male and female calves did not differ in time spent socializing (paired t test: female versus males, $t_{69.5} = 0.13$, $P = 0.90$), but calves of unknown sex socialized less than calves of known sex, probably because calf sex is typically determined during socializing when calves frequently go belly-up or have erections.

Although no meaningful sex differences were found in our overall analyses of the proportion of time that calves foraged and socialized, when the data set was limited to

Figure 1. The interaction between calf age class (1–4) and maternal presence–absence (i.e. the mother and calf were together versus separated) on calf foraging.

separations further than 50 m from the mother, female calves spent a greater proportion of time foraging than male calves $(\overline{X}_\mathrm{f} \pm \mathrm{SE} = 56.93 \pm 4.96\%; \overline{X}_\mathrm{m} \pm \mathrm{SE} = 43.00 \pm 4.90\%$; Mann–Whitney U test: $U = 251.5$, $N_\mathrm{f} = 28$, $N_\mathrm{m} = 29$, $P = 0.01$). However, we found no corresponding sex difference in socializing at far distances $(\overline{X}_\mathrm{f} = 15.11 \pm 5.20\%; \overline{X}_\mathrm{m} = 15.51 \pm 2.88\%$; Mann–Whitney U test: $U = 328.5$, $N_\mathrm{f} = 28$, $N_\mathrm{m} = 29$, $P = 0.21$).

What Factors Predict the Number of Calf Associates?

Together with mother

When a mother and calf were together, the number of associates was related to calf sex and the interaction between calf age and maternal foraging time (Table 4). Across all age classes, maternal foraging time was inversely related to the number of associates (Fig. 3). Although the differences between specific age classes varied in significance, the general pattern was that calves with moderate and high levels of maternal foraging time had fewer associates as they aged (Table 5, Fig. 3). The interaction between calf sex and maternal foraging time was

Table 3. Repeated measures ANOVA table for calves' proportion of time spent foraging and socializing

Independent variable	Foraging			Socializing		
	df	F	P	df	F	P
Calf sex	2, 222	1.18	0.3102	2, 87.8	5.67	**0.0048**
Calf age class	3, 297	7.43	**<0.0001**	3, 135	6.33	**0.0005**
Maternal presence–absence	1, 162	373.42	**<0.0001**	1, 201	0.79	0.3766
Sex∗age class	6, 293	0.93	0.4761	6, 149	0.25	0.9586
Sex∗maternal presence–absence	2, 162	0.33	0.7227	2, 202	1.82	0.1655
Age class∗maternal presence–absence	3, 162	10.58	**<0.0001**	3, 206	0.98	0.4029
Sex∗age class∗maternal presence–absence	6, 162	1.11	0.3575	6, 204	0.64	0.6966

The variable 'maternal presence–absence' refers to whether the calf was 'together with mother' or temporarily 'separated from mother'. Significant values ($P < 0.05$) are presented in bold.
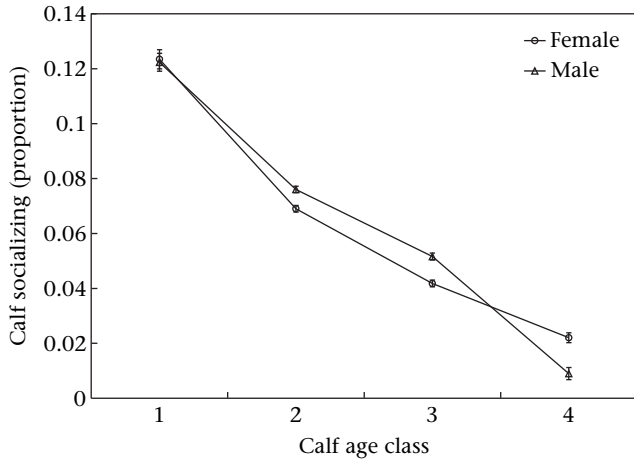
Figure 2. The proportion of time that calves in each age class spent socializing.

marginally nonsignificant (Table 4). When maternal foraging time was low, there was a tendency for female calves to have higher numbers of associates than male calves (paired t test: females versus males, $t_{130} = 1.80$, $P = 0.07$). This raises the question: are 'low foraging' mothers more social when they have female offspring than when they have male offspring? To partially answer this question, we compared mothers observed with at least one daughter and one son with similar hours of observation time. Offspring sex did not influence the number of associates (Wilcoxon signed-ranks test: $T = 28$, $N = 10$, $P = 0.54$) or maternal foraging time (female, $\overline{X} = 28.90 \pm 4.60\%$, median $= 25.50$; male, $\overline{X} = 21.50 \pm 5.40\%$, median $= 21.00$; $N = 10$; Wilcoxon signed-ranks test: $T = 14$, $N = 10$, $P = 0.10$) when claves were with their mothers. However, the latter result was inconclusive because of small sample size.
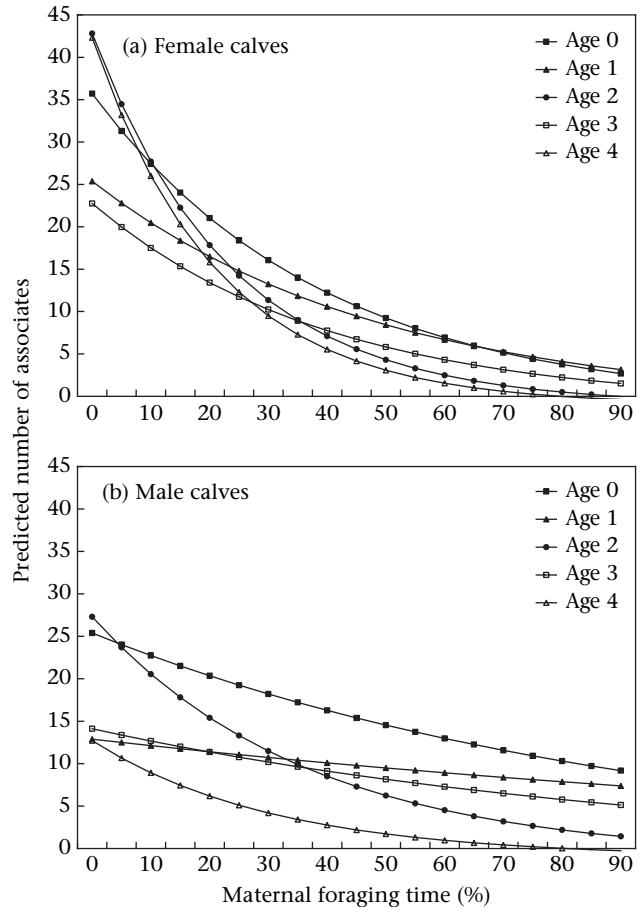
Separated from mother

A calf's number of associates during separations was positively related to both the percentage of time it spent

Figure 3. The interaction between calf age and maternal foraging time on the predicted number of associates while 'together with mother', shown separately for (a) female and (b) male calves. Partial regression equations were calculated for each age class, with 'calf hours observed' held constant at its mean (6.13 h).

separated from its mother and its associate number when with the mother (Table 6). Calves that spent more time separated from their mothers had more associates than calves that separated less (Fig. 4).

Table 4. Repeated measures ANOVA table for calves' number of associates while 'together with mother'

Independent variable	df	F	P
Calf sex	2, 75	4.20	**0.0186**
Calf age	4, 77	0.69	0.6020
Maternal foraging time	1, 103	21.60	**<0.0001**
Calf hours observed	1, 100	1.57	0.2128
Calf sex*age	8, 68	1.19	0.3164
Maternal foraging*calf sex	2, 79	2.67	0.0753
Maternal foraging*calf age	4, 102	4.72	**0.0015**
Maternal foraging*calf hours observed	1, 129	4.41	**0.0377**

The dependent variable, calf associate number, was log transformed to improve normality, and variance was grouped according to the sex of the focal calf. Nonsignificant ($P > 0.20$) two-factor interactions containing continuous variables were removed one at a time, in order of least significance, to arrive at the simplest model. Significant values ($P < 0.05$) are presented in bold.

Table 5. Pairwise means comparisons for calves' number of associates while 'together with mother': calf age*maternal foraging time

	Maternal foraging time (%)		
Age class comparison	Low (10.15)	Moderate (31.46)	High (52.77)
1 and 2	NS	NS	**<0.01**
1 and 3	NS	NS	NS
1 and 4	NS	**0.01**	**<0.001**
2 and 3	NS	NS	**0.03**
2 and 4	NS	0.06	0.07
3 and 4	NS	**0.01**	**<0.01**

P values are presented for each age class comparison at the three levels of 'maternal foraging time' that correspond with the mean $\pm$ 1 SD. Significant values ($P \leq 0.05$) are presented in bold. NS $= P > 0.10$. To control for variation in 'calf hours observed', this covariate was held constant at its mean (6.13 h) for these comparisons.

Table 6. Repeated measures ANOVA table for calves' number of associates while 'separated from mother'

Independent variable	df	F	P
Calf sex	2, 149	2.32	0.1020
Calf age	4, 149	1.33	0.2632
Maternal foraging time	1, 149	0.58	0.4491
Log calf % time separated	1, 149	17.22	**<0.0001**
Log calf associate no. 'together'	1, 149	86.99	**<0.0001**
Calf hours observed	1, 149	0.97	0.3257
Calf sex*age	8, 149	1.10	0.3697
Log calf % time separated*calf sex	2, 149	2.75	0.0669
Log calf hours observed*age	4, 149	2.31	0.0603

The dependent variable was log transformed to improve normality. Three continuous independent variables were also log transformed to improve linearity and model fit. Nonsignificant ($P > 0.20$) two-factor interactions containing continuous variables were removed one at a time, in order of least significance, to arrive at the simplest model. Significant values ($P < 0.05$) are presented in bold.

Overall (both maternal presence–absence categories and combined age classes)

When data were combined across all age classes and both categories of maternal presence–absence, maternal foraging time and the percentage of time that calves spent in groups had opposite effects on the total number of calf associates, resulting in a significant interaction between these two factors (Table 7). As expected, the total number of associates was inversely related to maternal foraging time and positively related to the percentage of time that calves spent in groups. Calf sex was not a significant factor (paired t test: females versus males, $t_{59} = 0.65$, $P = 0.52$).
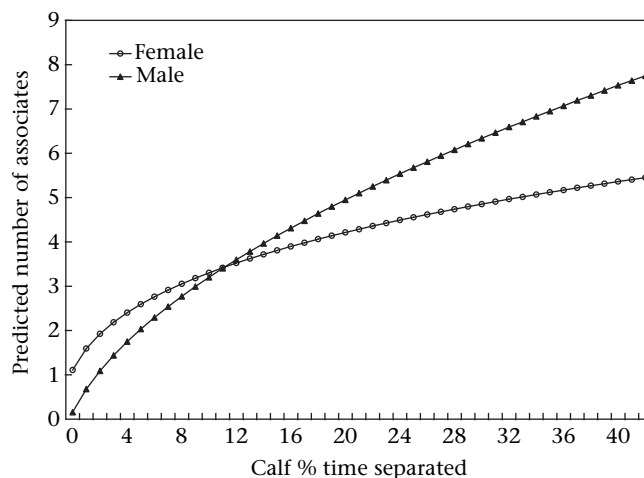
Figure 4. The interaction between calf sex and calf percentage of time separated on the predicted number of associates while 'separated from mother'. Partial regression equations were calculated with 'calf hours observed' (log transformed, 0.81 h), 'maternal foraging time' (31.68%) and 'calf associate number together' (log transformed, 1.12 associates) held constant at their respective means. The maximum value on the X axis was set at the 90th percentile.

Table 7. ANOVA table for calves' total number of associates

Independent variable	df	F	P
Calf sex	2, 57	4.97	**0.0103**
Maternal foraging time	1, 36	0.92	0.3444
Calf % time in groups	1, 31	0.07	0.7926
Calf hours observed	1, 56	0.90	0.3472
Maternal foraging time*calf % time in groups	1, 39	8.61	**0.0056**
Calf % time in groups*calf hours observed	1, 61	3.46	0.0676

The dependent variable was calves' total number of associates (i.e. 'together with mother' and 'separated from mother') combined across age classes 0–4. Nonsignificant ($P > 0.20$) two-factor interactions containing continuous variables were removed one at a time, in order of least significance, to arrive at the simplest model. Significant values ($P < 0.05$) are presented in bold.

What Factors Predict Calves' Percentage of Time in Groups?

Together with mother

As in our analysis of calves' associate numbers, the interaction between calf age and maternal foraging time was associated with the proportion of time that mothers and calves spent in groups (Table 8). Across all age classes, maternal foraging time was inversely related to the proportion of time that mother–calf pairs were in groups. But in contrast to the developmental pattern observed for calves' associate numbers, at low and moderate levels of maternal foraging time, time spent in groups increased with calf age (Table 9).

Separated from mother

During separations, the time that calves spent in groups was related to two interactions: calf sex × calf age and calf sex × calf percentage of time separated (Table 10). At low and moderate levels of calf separation, female calves were more sociable than male calves (paired t tests: low separation time: $t_{104} = 3.19$, $P = 0.0019$; moderate separation time: $t_{73} = 2.11$, $P = 0.0383$). Unlike our results for calves' associate numbers while separated, the relationship between separation time and time in groups differed

Table 8. Repeated measures ANOVA table for calves' percentage of time in groups while 'together with mother'

Independent variable	df	F	P
Calf sex	2, 112	0.88	0.4183
Calf age	4, 150	4.56	**0.0017**
Maternal foraging time	1, 146	65.18	**<0.0001**
Calf hours observed	1, 156	0.64	0.4233
Calf sex*age	8, 138	1.50	0.1643
Maternal foraging*calf age	4, 147	2.65	**0.0356**
Calf hours observed*age	4, 140	1.92	0.1097

The dependent variable was calves' percentage of time in groups (i.e. in association with others in addition to the mother). Nonsignificant ($P > 0.20$) two-factor interactions containing continuous variables were removed one at a time, in order of least significance, to arrive at the simplest model. Significant values ($P < 0.05$) are presented in bold.

Table 9. Pairwise means comparisons for calves' percentage of time in groups while 'together with mother': calf age*maternal foraging time

Age class comparison	Maternal foraging time (%)		
	Low (10.15)	Moderate (31.46)	High (52.77)
1 and 2	NS	NS	0.10
1 and 3	**0.02**	**0.04**	NS
1 and 4	**0.01**	NS	0.09
2 and 3	0.08	**0.02**	0.07
2 and 4	0.06	NS	NS
3 and 4	NS	NS	**0.05**

P values are presented for each age class comparison at the three different levels of 'maternal foraging time' that correspond with the mean ± 1 SD. Significant values (*P* < 0.05) are presented in bold. NS = *P* > 0.10. To control for variation in 'calf hours observed', this covariate was held constant at its mean (6.13 h) for these comparisons.

for female and male calves. As calves moved along the continuum from low to high separation time, sociality of female calves decreased. Conversely, in male calves, time spent in groups increased with separation time. Although the degree of difference varied between age classes, female calves generally spent less time in groups as they aged while males had no clear pattern (paired *t* tests: females, age class 1 versus 3, $t_{110} = 3.45$, $P = 0.0008$; age class 1 versus 4, $t_{112} = 2.10$, $P = 0.0376$; age class 2 versus 3, $t_{95} = 2.73$, $P = 0.0075$). In contrast to our results for calves' associate numbers, the proportion of time spent in groups while with the mother did not predict a calf's percentage of time in groups while separated (Table 10).

DISCUSSION

The primary goal of this study was to document the variability in the early social experiences of bottlenose dolphin calves and identify predictors of this variation. This is one of the few reports of associate number in

Table 10. Repeated measures ANOVA table for calves' percentage of time in groups while 'separated from mother'

Independent variable	df	F	P
Calf sex	2, 153	8.13	**0.0004**
Calf age	4, 145	3.25	**0.0138**
Maternal foraging time	1, 138	0.73	0.3957
Log calf hours observed	1, 158	0.26	0.6076
Calf % time separated	1, 162	1.36	0.2461
Calf % time in groups 'together'	1, 162	0.00	0.9447
Sex*age	8, 139	3.78	**0.0005**
Log calf hours observed*sex	2, 149	4.9	**0.0087**
Calf % time separated*sex	2, 160	4.85	**0.0090**
Log calf hours obs.*calf % time in groups 'together'	1, 154	2.85	0.0935

Nonsignificant (*P* > 0.20) two-factor interactions containing continuous variables were removed one at a time, in order of least significance, to arrive at the simplest model. Significant values (*P* < 0.05) are presented in bold.

bottlenose dolphins and is the first to examine the early patterns of sociality from birth until weaning in this species. Based on adult patterns previously reported (Smolker et al. 1992), we predicted and found that calves are exposed to a relatively large number of associates from an early age and that variation in sociality is substantial. Our findings provide insights into understanding the cognitive demands faced by calves within a complex fission—fusion society and selective pressures favouring a prolonged infancy period. Although closed or semiclosed communities are characteristic of the three species with fission—fusion patterns most similar to those found in bottlenose dolphins (i.e. spider monkeys, Symington 1990; chimpanzees, Goodall 1986; and humans, Rodseth et al. 1991), bottlenose dolphin communities appear to vary along an open—closed continuum (Wells et al. 1987; Smolker et al. 1992; Chilvers & Corkeron 2001; Lusseau et al. 2003). As a result, the number of potential social relationships is not necessarily restricted by community size. The 'social brain hypothesis' suggests that the cognitive demands of group life (e.g. the ability to maintain relationships) have selected for increased intelligence and, hence, larger brains (Byrne & Whiten 1988; Dunbar 1998). Most analyses of brain size evolution have used social group size or the total number of relationships maintained as a rough measure of social complexity, presumably because the number of relationships that are simultaneously maintained determine the cognitive demands placed on an individual (Joffe & Dunbar 1997). Thus, our analysis of total associate number in bottlenose dolphin calves and their mothers facilitates comparisons between taxa on the approximate number of relationships maintained during early development. However, in ungulates, the most closely related taxa to cetaceans, the nature of social relationships is more strongly correlated with brain (and neocortex) size than is group size (Schultz & Dunbar 2006), and may therefore provide a greater measure of the cognitive demands faced by an individual. Although no other studies have specifically examined the number of associates for other infant mammals, the average number of associates for dolphin calves is comparable to the mean group sizes (synonymous with community size) of the largest primate groups (Sawaguchi & Kudo 1990; Dunbar 1992; Barton 1996; Kudo & Dunbar 2001). Furthermore, since dolphin calves can 'choose' from a large number of associates during separations, they may face greater social (and cognitive) challenges from an early age than primate infants, where group size is either relatively constant or determined by the mother.

Although the number of calf associates in the first 4 years of life in our study ranged from 0 to 77 (unadjusted for hours observed), this is an underestimate because associate number was highly correlated with observation hours. Our results also underestimate the number of adult female associates, not only because of hours of observation, but also because lactating females avoid male associates (Gibson & Mann, in this issue). For example, the most social mother in our study was observed with 139 individuals over 11 years and with five calves. However, our sighting records on this female (155 sightings), which span 19 years and several reproductive states,

indicate that she has had at least 224 unique associates. When we divided the number of associates by the number of years observed, this female's number of associates per year was similar for survey (11.8 associates/year) and focal data (12.6 associates/year). Thus, although our focal data accurately capture the relative sociality between females and between calves, these estimates are influenced by hours of observation. This is probably true for sighting records as well. We hope that other studies examining sociality in bottlenose dolphins will take note of the substantial amount of data necessary to accurately assess basic social patterns.

Do Calf Activity Budgets Change with Calf Sex and/or Age?

As calves aged, they spent more time separated from their mothers, foraged more, and socialized less. These findings are consistent with previous studies on this population (Mann & Sargeant 2003; Mann & Watson-Capps 2005). However, this is the first analysis of socializing throughout the calf period. Although the proportion of time spent socializing did not change within the first year of calf life (Mann & Watson-Capps 2005), our results indicate that calf socializing peaks during the first year and steadily decreases thereafter. Thus, the first year may be particularly important for gaining experience in social interactions (play and other affiliative behaviours).

Calves spent a greater proportion of time foraging while separated from their mothers than while with them, which is also consistent with a previous study that focused on the first year only (Mann & Watson-Capps 2005). Although male and female calves did not differ in the overall proportion of time spent foraging or socializing, female calves spent more time foraging while on far separations than did male calves. Calves, especially females, appear to devote more time to developing foraging skills as they approach weaning age. This is consistent with previous findings that females, more than males, show diverse foraging tactics (Mann & Sargeant 2003; Sargeant et al. 2005).

Are the Two Sociality Measures Related?

As predicted, our analysis of calves' total associate numbers indicated that the two sociality measures, number of associates and percentage of time in groups, are related: calves that were highly social by one measure were also highly social by the other. Although the predictors of calf sociality differed depending on the measure used and whether a calf was with its mother or temporarily separated from her, there was consensus between the two measures. When calves were with their mothers, calf age and maternal foraging time were important predictors of both the number of associates and the proportion of time in groups. As maternal foraging time increased, the sociality of a mother–calf pair (by either measure) decreased. In contrast, the relationship between calf age and sociality while with its mother differed depending on the measure used. As calves aged, their number of associates decreased but their percentage of time in groups increased, suggesting that the identity of their associates may have stabilized. During mother–calf separations, the proportion of time separated was an important predictor of calf sociality. However, the relationship between calf separation time and sociality differed depending on the measure used and the sex of the calf. As calf separation time increased, associate number increased for both male and female calves, but the percentage of time in groups increased for males and decreased for females. We will discuss this pattern in more detail below.

Do Calf Sex and Age Predict Sociality?

The negative relationship between maternal foraging time and mother–calf sociality was expected. Foraging is a predominantly solitary activity. Although calves are most likely to separate during maternal foraging bouts (Mann & Smuts 1998; Mann & Watson-Capps 2005), maternal foraging probably determines maternal social patterns. In particular, adult females that engage in foraging tactics that require a relatively high time investment (see Mann & Sargeant 2003) have less time available to be in groups. The marginally nonsignificant interaction between calf sex and maternal foraging time was unexpected. Among mothers with low foraging budgets, female offspring tended to have more associates than male offspring. However, our test of whether offspring sex influenced maternal foraging time revealed that this does not appear to be the case.

With age, calves generally decreased their associate number but increased their time in groups. Possibly, group sizes are larger when calves are younger and more vulnerable to predation (Mann et al. 2000; Mann & Watson-Capps 2005) or more individuals are attracted to young calves (Mann & Smuts 1998). In addition, as calves approach weaning, adult male interest in their mothers is likely to increase. Adult males may remain with a cycling female for prolonged periods during consortships (Connor et al. 1996), thereby dramatically increasing the proportion of time that a mother and calf are in groups. Analyses of group size and composition have revealed that mother–calf groups contain the highest proportion of adult males when calves are in age class 3. However, this does not explain the same pattern during mother–calf separations.

Calf social patterns during separations are related to the calf's tendency to separate in the first place, and the calf's sex and age. Associate number increased with separation time for both male and female calves. This result may simply be a by-product of highly independent calves having more opportunities to encounter other dolphins. Yet, the pattern for calf time in groups is more complicated. While separated, female calves decreased their amount of time in groups with age, but males did not. This decrease in sociality for female calves was probably related to their increased foraging time, a pattern more marked for females than males. Contrary to our expectation that male calves would engage in more social separations than female calves, less independent (low–moderate separation time) female calves spent more

time in groups during separations than males. Perhaps among less independent calves, females are more likely than males to associate with nearby maternal associates, possibly kin, during separations. But as calves moved along the continuum from low to high separation time, males spent more time in groups, but females spent less. Perhaps this conflicting relationship between calf independence and sociality for males and females reflects their different sex-specific socioecological requirements. Male calves that are more independent show increased sociality, enabling them to become acquainted with other males. In contrast, more independent female calves have decreased sociality, possibly because they devote more time to mastering the foraging tactics of their mothers (see Mann & Sargeant 2003). This explanation is supported by our finding that female calves foraged more often than male calves during far separations, another indicator of calf independence.

Does Sociality with the Mother Predict Sociality During Separations?

Maternal social patterns were expected to influence calf social patterns during separations, but only calf associate number, and not time in groups, was related to the mother's social pattern. Perhaps this is an indication that a calf encounters associates from its mother's network during separations, but patterns his or her time with others differently than its mother. For example, while with their mothers, calves spend considerable time in groups with adult females because these individuals are the preferred associates of the mother (Gibson & Mann, in this issue). During separations the calf may encounter these same adult females but spend less time with them. Analyses of calf group composition and associate identity are necessary to determine whether calves preferentially associate with maternal associates. But based on our results, it appears that some maternal social patterns (i.e. number of associates) are readily adopted by the calf. Alternatively, mothers with more associates may be in areas with more available associates. Thus, their calves may have more individuals to join with during separations. Primate studies have shown that infants will continue to associate with individuals from their mothers' social networks even when interacting independently of them, but within the same group (Berman 1982; de Waal 1996). Although the mechanisms for the transmission of social patterns from mother to offspring have not yet been identified, it seems likely that early social exposure (i.e. familiarity) and active maternal influence are involved (de Waal 1996). Comparison between this study and those of other social species is difficult because most studies of early mammalian social development involve species with stable group structure, low variation in social patterns and offspring that do not have independent associates.

Conclusion

Our analyses of individual variation in calf sociality are a first step in identifying how social patterns form in bottlenose dolphins. Although maternal socioecological strategies shape the social patterns of offspring, the impact is likely to be different for males and females. For example, males born to relatively solitary mothers may be at a distinct disadvantage in their ability to develop strong bonds with other males, and eventually form alliances. The daughter of a solitary mother would not be similarly disadvantaged since group size does not predict female reproductive success (Mann et al. 2000), and because daughters probably adopt their mother's foraging style (see Mann & Sargeant 2003). Long-term study will reveal the effects of these different socioecological strategies on lifetime fitness. In addition, future analyses on calf group size, group composition and associate identity will refine the interpretation of these results and enable a better understanding of social development in bottlenose dolphins.

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