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The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia

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The fission–fusion society of bottlenose dolphins seems particularly well suited to balancing the costs and benefits of grouping. Here, we examined four nonmutually exclusive hypotheses regarding the causes and/ or functions of calf grouping patterns when with and away from the mother: maternal influence, same-sex bond formation, protection and social skill development. We evaluated the role of calf (calf sex, age and separation from their mothers) and maternal characteristics (foraging time and sociality) in shaping the size and composition of mother–calf groups using focal observations of 49 mothers and 89 calves. Mother–calf groups were biased towards association with females of all ages and with male calves, but contained relatively few juvenile and adult males. Although there was some support for all of the hypotheses, the social skills hypothesis best explained male calf social patterns, and maternal influence better explained female calf social patterns. While maternal sociality influenced calves of both sexes, daughters mirrored the mother during separations, whereas sons did the opposite, seeking more social contact if their mothers were solitary and seeking less social contact if their mothers were sociable. During mother–calf separations, calves of both sexes preferentially associated with immatures over adults, but male calves preferred juvenile and adult male associates, which female calves, like their mothers, avoided. Calf social patterns illustrate the specific social and ecological challenges that they face in relation to and independent of their mothers.

Mammalian social evolution is typically explained by species-specific ecological pressures (e.g. resource distribution and predation) and social pressures (e.g. male harassment, competition and infanticide risk), and in particular, how these factors influence female grouping and reproduction (Alexander 1974; Wrangham 1980, 1987; van Schaik 1989). Demographic factors (e.g. availability of social partners and population density) also interact with grouping patterns to determine within-group competition levels and ultimately the social relationships among members (Sterck et al. 1997; Barrett & Henzi 2002). Finally, the distribution of males is jointly affected by the distribution of females and by the role of male–female relationships in protection of offspring (Wrangham 1987; Sterck et al.

1997). Although such models focus primarily on factors that drive adult grouping, similar pressures (e.g. predation risk and availability of social partners) probably influence the grouping patterns of immatures as well. Here we take a novel approach by examining the function(s) of bottlenose dolphin mother–calf sociality from the calf's perspective, a task facilitated by the dolphin calf's tendency to separate frequently from the mother, associate with others independently, and thus emulate the fission–fusion character of the society at large (e.g. Mann & Watson-Capps 2005; Gibson & Mann 2008).

Several ungulate, primate, delphinid and carnivore species show a fission–fusion social organization in which group size and composition are temporarily and spatially variable (Goodall 1986; Packer 1986; Symington 1990; Holekamp et al. 1997; Connor et al. 2000; Archie et al. 2006). In this type of society, patterns of association are likely to be tightly linked to social and ecological contexts, and can thus help identify the costs (e.g. intragroup

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feeding competition; Wrangham 2000) and benefits (e.g. protection from predation or conspecific aggression; van Schaik 1989) of grouping. Like most social mammals, bottlenose dolphins preferentially associate with members of the same sex, a pattern likely to reflect the different reproductive strategies of males and females (Wells et al. 1987; Smolker et al. 1992; Connor et al. 2000; Krützen et al. 2004). Males form long-term alliances, allowing them to better compete for females (Connor et al. 1992, 1999; Owen et al. 2002; Parsons et al. 2003). Females form loose social networks with other females of varying age and kinship (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006); their relationships can be characterized as socially tolerant (Scott et al. 2005). Females range from being almost solitary to highly gregarious (Smolker et al. 1992; Gibson & Mann 2008); such variation is probably driven by ecological factors (e.g. foraging tactics, Mann & Sargeant 2003), but the benefits of female grouping are not well understood. For example, average group size does not predict female calving success, but habitat use does (Mann et al. 2000).

With low locomotion costs compared to terrestrial mammals (Williams et al. 1992) and fluid grouping patterns, bottlenose dolphins can avoid direct resource competition and aggregate between foraging bouts. In Shark Bay, Australia, females do not cooperatively defend food patches (Mann & Sargeant 2003) or share prey (Mann et al. 2007), and predation is unlikely to be the primary cause of calf mortality (Mann & Watson-Capps 2005); thus the benefits of female grouping may be social in nature (e.g. reduced male harassment, calf care, social learning or bond formation). However, even if predation is not the primary pressure favouring grouping, risk of shark attack is still likely to influence grouping patterns and habitat use (Heithaus & Dill 2002). For example, females with newborns occur in larger groups than when their calves are older (Mann et al. 2000), and mothers and calves are most sociable during the calves' first year (Gibson & Mann 2008), when mortality rate is highest (Mann et al. 2000).

In mammals with long periods of dependency and complex social systems, social relationships (both long and short term) probably originate in infancy (e.g. MacKinnon 2007). Although Shark Bay bottlenose dolphin calves nurse for 3–8 years (Mann et al. 2000), they are highly precocial and begin catching fish at 4 months (Mann & Smuts 1999; Mann & Sargeant 2003). Furthermore, despite the benefits of maternal protection, calves temporarily separate from their mothers, frequently and often to far distances, from an early age, regardless of season and predation risk (Mann & Smuts 1999; Mann & Watson-Capps 2005; Gibson & Mann 2008). Calves forage and socialize more often during separations than when they are with their mothers (Mann & Watson-Capps 2005; Gibson & Mann 2008). The calf's tendency to separate is unusual among mammals with long periods of dependency and provides us with a rare opportunity to investigate calf social patterns and associations when with and when separated from the mother. This enables us to determine whether patterns of adult female and calf association reflect maternal or calf interests. We examined four nonmutually exclusive hypotheses regarding the causes and functions of calf groups: maternal influence, same-sex bonds, protection and social skills. Our hypotheses and specific predictions are presented in detail below and outlined in Table 1 for clarity.

Maternal Influence Hypothesis

A calf necessarily experiences the same social environment as the mother most of the time, but has distinct social options during separations. The maternal influence hypothesis broadly suggests that calves will show social tendencies similar to their mothers during separations (time alone, time in large groups, sex–age class association preferences), simply because this is what they are exposed to and learn to emulate (proximate mechanism). Although we would expect these relationships to hold for offspring of both sexes, we predict that daughters would emulate their mothers more than sons. Females, more than males, would be likely to benefit by adopting the foraging and social tactics of their mothers, and previous research points in that direction (Mann & Sargeant 2003; Sargeant et al. 2005; Gibson & Mann 2008). Because maternal foraging is likely to determine social patterns, especially for females, we included this factor in all of our models.

Same-sex Bonds Hypothesis

Both sexes show natal philopatry, but female kin associations persist postweaning (southeastern Australia: Möller et al. 2006), and males are reported to associate primarily with male juveniles (Sarasota, Florida, U.S.A.: Wells et al. 1987; Wells 1991). In Shark Bay, some males that played together extensively as calves were still being sighted together 15 years later (Mann 2006), when alliances are thought to stabilize (Connor et al. 2000). In Sarasota, Florida, males appear to form alliances in their early teens (Owen et al. 2002). Thus, male and female calves may preferentially associate with individuals of the same sex in the interest of establishing long-term bonds. Previous research shows that calves decrease the number of associates with age, but increase the proportion of time in groups, suggesting that long-term, stable relationships might be forming (Gibson & Mann 2008).

Protection Hypothesis

Bottlenose dolphin groups containing females and calves are often referred to as 'nursery' groups (e.g. Wells et al. 1987; Wells 2003), implying that these groups cooperate to provide protection and/or social opportunities for calves. Wells (2003) proposed that females in large, stable nursery groups might have higher reproductive success than lone females, a pattern not found in Shark Bay (Mann et al. 2000). Predation risk influences dolphin habitat use and grouping in Shark Bay (Heithaus & Dill 2002), but this relationship is not similarly straightforward for mothers and calves (Mann et al. 2000; Mann & Watson-Capps 2005). For example,

Table 1. Hypotheses and predictions regarding the function of calf groups

Maternal influence hypothesis
Group size predictions
  (1) Proportion of time on solitary separations is related to proportion of time that mother—calf pair spends alone; relationship stronger for daughters than for sons
  (2) Proportion of time in large groups during separations is related to proportion of time that mother—calf pair spends in large groups
Group composition predictions
  (3) Relative proportion of each age—sex class in groups is similar when with and when separated from mother

Same-sex bonds hypothesis
Group composition predictions
  (1) Proportion of same-sex immature associates in groups is higher during separations than when with mother; difference is greater for male calves than for female calves
  (2) Proportion of same-sex immature associates in groups increases with age

Protection hypothesis
Group size predictions
  (1) Increase in proportion of time on solitary separations (alone) with calf age (antipredation)
  (2) Decrease proportion of time in large groups with calf age (antipredation)
Group composition predictions
  (3) Proportion of adult and juvenile females in groups during separations is the same as or higher than that when with mother (antipredation and/or conspecific harassment)
  (4) Proportion of adult and juvenile males in groups during separations is the same as or lower than that when with mother (conspecific harassment)

Social skills hypothesis
Group size predictions
  (1) Female calves spend a similar proportion of time in large groups when with and when separated from their mothers, regardless of their mothers' degree of sociality
  (2) Male calves with relatively solitary mothers spend more time in large groups when separated than do male calves with more social mothers
Group composition predictions
  (3) Proportion of immature associates, particularly immature males, in groups is higher during separations than when with mother

calf group size tends to be smaller when predation risk is high in the warm months than when predation risk is low in cooler months (Mann & Watson-Capps 2005), even though 34% of calves (Mann & Barnett 1999) and 74% of noncalves in Shark Bay have shark bite scars (Heithaus 2001).

Lone calves also risk encountering potentially dangerous juvenile or adult males. Although infanticide has not been observed in Shark Bay bottlenose dolphins, males are much more aggressive than females (Scott et al. 2005) and infanticide has been reported elsewhere (Patterson et al. 1998; Dunn et al. 2002). Thus, the fact that calves engage in frequent solitary separations despite the apparent risk of predation and conspecific aggression, leads us to question whether grouping serves a protective function. If grouping protects calves, then the proportion of time that calves spend in large groups would decrease as calf age increases and vulnerability decreases. Similarly, the calves are predicted to spend more time alone as they age.

Groups containing adults are likely to offer calves more protection (via active defence or deterrence) than groups containing immatures only. However, if risk of conspecific aggression is more influential than predation, then the sex of associates also becomes important. We would predict that the proportion of adult and juvenile females in calf groups would be the same or higher during separations than when claves are with their mothers because these are the age—sex classes that are likely to offer the most protection and be least aggressive. The proportion of adult and juvenile males in calf groups is predicted to be the same or lower during separations than when calves are with the mother. We assume that male and female calves are equally vulnerable to predation or male aggression and predict no sex difference in grouping under the protection hypothesis.

Social Skills Hypothesis

Early social interactions may aid in the development of agonistic or affiliative skills for concurrent or future use (Pereira & Fairbanks 1993). Grouping may enable calves to develop and practice these skills before they incur the costs of direct reproductive competition. Most mammalian studies show that immature males play more often and engage in mock fighting more than females (reviewed in Byers 1984; Meaney et al. 1985), suggesting that the skills obtained through rough play with peers (e.g. fighting ability) are essential for males. Sociosexual and fighting skills may be necessary to function within a male alliance, which can include up to 14 dolphins (Connor et al. 1999). Sociosexual behaviour of male calves resembles adult male alliance patterns in that their interactions are often symmetrical, synchronous and involve multiple males; calves of both sexes also mimic the courtship behaviour of adults (Mann 2006). Thus, early social experience might influence the ability of males to form and maintain alliances. Male calves born to relatively solitary mothers could then be at a disadvantage; if social skills are vital, they are predicted to seek out more social opportunities during separations than males that have sociable mothers. Female calves may also benefit by participating in sociosexual interactions (mock courtship) with young males. But because female calves are likely to adopt maternal patterns, they probably obtain sufficient social exposure when they are with their mothers, regardless of their mothers' degree of sociality. Play fighting and sociosexual skills may be less critical for females than males. Conversely, foraging skill development may be more critical for females than males.

Since play most often occurs among age peers (Lee 1986; Pusey 1990; Rothstein & Griswold 1991; Thompson 1996) and is biased towards males (reviewed in Meaney et al. 1985), we would expect the proportion of immature associates, particularly immature males, to be higher during separations than when calves are with their mothers for both sexes. This hypothesis differs from the same-sex bonds hypothesis in that both male and female calves are expected to increase association with male immatures, rather than immatures of the same sex. In addition, the social skills hypothesis does not predict a decrease in associate number with age.

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 ideal 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 consists of over 1200 individually recognized bottlenose dolphins (*Tursiops* sp.) since 1984. Species status is not resolved because Shark Bay bottlenose dolphins show *truncatus* and *aduncus* haplotypes (M. Krützen & W.B. Sherwin, unpublished data). 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). Since the average water depth in Shark Bay is 5–6 m, dolphin foraging and social behaviours are typically visible from the surface. Foraging behaviours can also be inferred from movement (e.g. fast swims, rapid direction changes) accompanied by fish catches and observations of fish fleeing. Group composition was scanned for mother and calf every minute during focal follows; all joining and leaving events were recorded on a continuous basis. 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 a calf was more than 10 m from its mother and no other dolphins were linking them by 10 m. Distance estimates were facilitated using dolphin body lengths (~2 m), boat lengths (4.5 m), a laser rangefinder and global positioning system (GPS) tracking. During temporary mother–calf separations, we stayed with the calf but continued data collection for the mother whenever possible.

Our analyses include focal data for calves, from birth through weaning, collected during the period of 1989–2006, but they exclude data on calves older than 4 years because of low sample sizes. Four years is the average

weaning age for bottlenose dolphins in Shark Bay (Mann et al. 2000). For calves weaned prior to age 4, postweaning data were excluded. Only calves that were observed for more than 1 h in at least one age class were included. These criteria generated a total of 1165.3 h of focal calf data (1157.9 h for mothers). When age class 0 was excluded, as in our group size analyses, calves were observed 5.64 ± 0.35 h ($N = 84$) per age class and spent $17.52 \pm 1.73\%$ ($N = 84$) of their time separated from their mothers.

Sex and Age Determination

Data were subgrouped according to the sex and age class of each focal calf at the time of observation. The sex of focal calves and their associates was determined primarily by opportunistic views of the genital region. In a few cases, sex was determined 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, an age estimate was made on the basis of physical and behavioural characteristics such as the presence of fetal folds or lines, surfacing behaviour, and size in relation to the mother. Young of the year, seen between 4–11 months of age when newborn traits had vanished, were assigned a default birthday of 1 November, when births peak (Mann et al. 2000). All calves in this study had birthdate estimates that were accurate within 6 months, but most were accurate within weeks. All age classes could be assigned with certainty (Table 2). 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 its mother and when the mother–calf association decreased to less than 50%. Immediately following weaning, mother–offspring association averages 25.3% of the time (Mann et al. 2000). The age of calf associates, unless a birthdate was known, was estimated based on body size, degree of ventral speckling and/or the birth of a first calf (see Smolker et al. 1992 for additional details). Associates were assigned to age categories according to the criteria in Table 3.

Group Size

Calf group size was examined in terms of the proportion of time spent alone and the proportion of time spent in large groups. For each of these measures, a separate analysis was conducted for the subcategories of 'together

Table 2. 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 3. Sex specific age class definitions for associates

Age category	Sex	Age range (years)
Calves	Female	0−3.99
	Male	0−3.99
Juveniles	Female	4−11.99
	Male	4−13.99
Adults	Female	12+
	Male	14+

with mother' and 'separated from mother'. These two subcategories provide a comparison of the calf's independent association patterns and those assumed to be maternally driven. Because of our interest in the social stimulation available to the calf, we calculated group size as the number of individual dolphins in the group in addition to the mother and calf. We excluded from our analyses minutes in which group size was uncertain, except when it was known that at least seven individuals were present. These groups were included to prevent a bias against large groups since exact group size is easier to determine in small groups.

Because calf group sizes are likely to vary considerably depending on whether a calf is with its mother or temporarily separated, we calculated the upper quartiles for average calf group sizes when 'together with mother' and when 'separated from mother' and used those numbers to define 'large groups'. To clarify, the upper quartile for average calf group size was 4.27 when calves were 'together with mother' ($\overline{X} = 2.56 \pm 0.23$, range 0−11, $N = 89$). Because the upper quartile was more than four dolphins, calf groups containing five or more associates in addition to the mother were considered 'large groups'. Likewise, the upper quartile for average calf group size when 'separated from mother' was 0.98 ($\overline{X} = 0.67 \pm 0.09$, range 0−6.21, $N = 82$). Thus, we considered cases where the calf was in a group with two or more associates as a 'large group' during separations.

To examine predictors of calf group size and test our hypotheses, we conducted four separate analyses (one for each of the categories listed above) using generalized linear mixed models (Proc Glimmix, SAS v. 9.1, Cary, NC, U.S.A.). We selected this method because of its ability to fit statistical models to data with correlations, heterogeneous variances and non-normal distributions. In all four analyses, the distribution was defined as binomial with the link defined as logit (i.e. log of odds ratio). The chi-square fit statistics were used to assess model fit (over- or underdispersion of variance). Means and their standard errors were converted back to the original scale (inverse link). The reported standard errors were calculated by the delta method (similar to the jackknifing technique). Sample sizes varied by analysis since not all calves were observed during separations and because age class 0 had to be excluded because of small sample sizes in each category. As a result, our analyses of calf group size included 84 calves (47 mothers) when 'together with mother' and 79 calves (43 mothers) when 'separated from mother'.

For the two models examining calf group size when 'together with mother', the dependent variable was either the proportion of time spent alone or the proportion of time spent in large groups. Independent variables include calf sex, calf age class, their mothers' percentage of time foraging and the number of hours that a calf was observed. Maternal foraging time (percentage of 1 min point samples that the mother was foraging) was included as a potential predictor of calf group size because previous analyses indicated an inverse relationship between maternal foraging time and calf sociality (i.e. number of associates and percentage of time in groups; Gibson & Mann 2008). In the two models examining calf group size when 'separated from mother', the dependent variable was again either the proportion of time spent alone or the proportion of time spent in large groups. In addition to the independent variables listed above, these models included the proportion of time that a calf spent separated from its mother (a measure of calf independence) and either a calf's proportion of time alone or proportion of time in large groups when with its mother (used as a proxy for maternal sociality). All analyses were first conducted using complete second-order models; all possible two-way interactions were included. 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. 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 (mean − 1 SD), moderate (mean), and high (mean + 1 SD) levels of these factors. Estimate statements (SAS v. 9.1) were used to obtain slopes and intercepts for partial regression equations and to conduct tests of hypotheses.

Group Composition

We began our investigation of age- and sex-specific patterns of association by examining the proportion of each possible age−sex category in calf groups. Associates whose identity was unknown were included in these analyses and coded to reflect age or sex information, if known. Only minutes in which a calf was in association with at least one individual besides its mother were included in the data set. This resulted in 556.35 h of group composition data for 85 calves, age classes 0−4. Four calves (out of 89 total) were excluded from the data set because they were never observed in association with individuals other than their mother.

Preferences for associates of specific age−sex categories, with respect to their availability, were determined by testing the observed proportions of each age−sex category in calf group compositions against the average proportion of each age−sex category in the population. These proportions were calculated using all known males and females that we identified in the Shark Bay population over a 10-year period. The proportion of males and females in each age class was calculated for each year

and averaged over 10 years. The age–sex class structure of the population never varied more than 2% for any category from year to year. Observed values were standardized by subtracting the reference value (population averages of each age–sex category) from the observed values. The mean of these difference scores was then tested against zero via a t test.

Calf patterns of association were examined using a generalized linear mixed model (Proc Glimmix, SAS v. 9.1), which allows for correlated data, nonconstant variability and non-normal distributions. As with our group size analyses, the distribution was defined as binomial with a logit link function, and the chi-square fit statistics were used to assess model fit. To control for variation in observation time per calf, data were weighted according to the number of minutes per maternal presence–absence category within each age class for a calf. Means and their standard errors were converted back to the original scale (inverse link). The reported standard errors were calculated by the delta method. In these models, the dependent variable was the average proportion of each possible age–sex category in calf group compositions. Thus, six separate analyses were conducted to examine calf association with adult females, adult males, juvenile females, juvenile males, female calves and male calves. Each analysis was conducted using a complete second-order model, including all two-way interactions, and independent variables were calf sex, calf age and maternal presence–absence in the group. Pairwise means comparisons were conducted only for ANOVA effects with a $P \leq 0.10$.

RESULTS

Calf Group Size

Average group size for calves (excluding mother and calf), with age class 0 included, was 2.28 ± 0.22 (range for mean group sizes 0–11; range for all groups 0–19; $N = 89$ calves). When age class 0 was excluded (as in the following analyses), mother and calf were together but without additional associates $51.31 \pm 3.21\%$ ($N = 84$) of the time and calves were completely alone $69.87 \pm 2.88\%$ ($N = 79$) of the time during mother–calf separations. Overall, calves spent $54.17 \pm 3.12\%$ ($N = 84$) of their time alone (excluding consideration of the mother). The mean proportion of time that calves spent in large groups was $21.77 \pm 2.31\%$ ($N = 84$) when with their mothers and $14.39 \pm 1.82\%$ ($N = 79$) when separated. The mean percentage of time spent in large groups overall was $20.79 \pm 2.05\%$ ($N = 84$).

Proportion of Time Alone

Predictors of time that mother–calf pairs spent alone

First, we examined which factors predicted the amount of time that mother–calf pairs spent alone. Both maternal foraging time and calf sex interacted with calf age to influence the proportion of time that mothers and calves spent alone (Table 4). Maternal foraging time averaged $33.63 \pm 2.27\%$ ($N = 84$). As maternal foraging time increased, mother–calf pairs spent more time alone.

Table 4. Results from the repeated measures ANOVA for the proportion of time that mother–calf pairs spent alone

Independent variable	df	F	P
Calf sex	2, 95	1.58	0.2123
Calf age	3, 131	5.47	**0.0014**
Maternal foraging time	1, 148	63.7	**<0.0001**
Calf hours observed	1, 148	0.02	0.8779
Calf sex×age	6, 118	2.16	**0.0519**
Maternal foraging time×age	3, 126	2.85	**0.0403**
Calf hours observed×age	3, 122	3.26	**0.0240**

The dependent variable, proportion of time that mother–calf pairs spent alone, represents the proportion of time that the mother and calf were together but not in association with other dolphins. 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 ($P \leq 0.05$) are presented in bold.

However, regardless of how much time mothers spent foraging, mothers and calves showed a general pattern of spending less time alone as calf age class increased from 1 to 3 (Table 5). The increase in the proportion of time spent alone with maternal foraging was greater in age class 4 than in other age classes (Table 5). The only sex difference occurred in age class 3, when mothers and daughters spent less time alone than mothers and sons (independent t test: $t_{136} = -2.17$, $P = 0.03$).

Predictors of time that calves spent alone during separations

Solitary separations were related to a number of interactions: calf sex × calf age, calf sex × percentage of time separated, maternal foraging time × calf age, and percentage of time separated × percentage of time alone while with mother (Table 6). Within age classes, the only sex difference occurred during age class 3 in which female calves spent more time alone than male calves (independent t test: $t_{116} = -3.01$, $P < 0.01$; Fig. 1), precisely opposite to the pattern observed when with their mothers. Both sexes spent more time alone in age class 4 than in age class 1 (independent t test: female calves,

Table 5. Proportion of time that mother–calf pairs spent alone: maternal foraging time × calf age class

| Age class comparison | Maternal foraging time | | |
	Low (10%)	Moderate (31%)	High (53%)
1 vs 2	0.5605	0.3730	0.0653
1 vs 3	**0.0148**	**0.0172**	0.3574
1 vs 4	**0.0095**	0.4018	0.1657
2 vs 3	0.0588	**0.0040**	**0.0181**
2 vs 4	**0.0305**	0.1606	0.9280
3 vs 4	0.4715	0.3642	**0.0530**

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

Table 6. Results from the repeated measures ANOVA for the proportion of time that calves spent alone during separations from their mothers

Independent variable	df	F	P
Calf sex	2, 108	6.29	**0.0026**
Calf age	3, 103	0.9	0.4439
Maternal foraging time	1, 96	7.21	**0.0085**
Calf hours observed	1, 100	0.07	0.7941
Calf % time separated	1, 121	16.6	**<0.0001**
Calf % time alone with mother	1, 111	27.44	**<0.0001**
Calf sex×age	6, 96	2.34	**0.0374**
Calf hours observed×sex	2, 106	2.62	0.0777
Calf % time separated×sex	2, 124	11.64	**<0.0001**
Maternal foraging time×age	3, 93	2.92	**0.0381**
Calf % time separated×age	3, 102	1.74	0.1645
Calf % time alone with mother×age	3, 90	2.14	0.1010
% Time separated×% time alone with mother	1, 115	6.63	**0.0113**

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 ($P \leq 0.05$) are presented in bold.

age class 1 versus 4, $t_{94} = -2.26$, $P = 0.03$; male calves, age class 1 versus 4, $t_{71} = -2.62$, $P = 0.01$; Fig. 1). Female calves also spent more time alone in age class 3 than in age classes 1 and 2 (independent t test: age class 1 versus 3, $t_{86} = -4.36$, $P < 0.0001$; age class 2 versus 3, $t_{78} = -3.25$, $P < 0.01$). That is, female calves engaged in more solitary separations with age, but for male calves, this was evident only when comparing the older classes to the youngest age class, when calves and mothers are most sociable. Among calves that separated often, female calves spent more time alone than male calves (independent t test: female versus male, $t_{103} = 2.15$, $P = 0.03$; Fig. 2). During age classes 2 and 4, solitary separation time was inversely related to maternal foraging time.
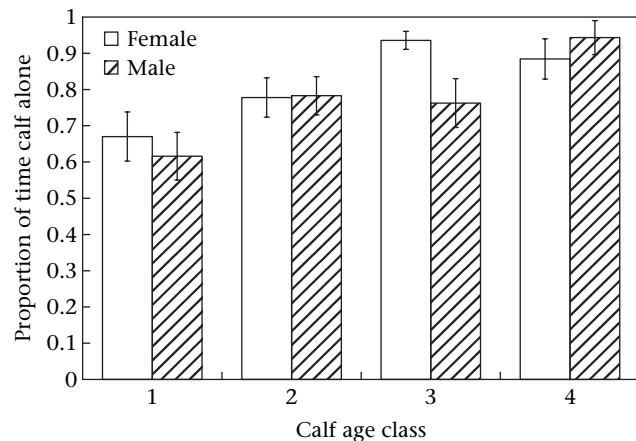
Maternal foraging time was not related to solitary separations for age classes 1 and 3. Among relatively asocial mother−calf pairs (i.e. high percentage of time alone), the calves that separated more often also had more solitary separations (Fig. 3).

Proportion of Time in Large Groups

Predictors of mother−calf pairs time in large groups

As with time alone, the proportion of time that mothers and calves spent in large groups was related to the interaction between maternal foraging and calf age (Table 7). The proportion of time that mother−calf pairs spent in large groups decreased as maternal foraging time increased (Fig. 4). In general, mothers and calves spent the most time in large groups when the calf was in age class 3 and the least during age class 4 (Table 8, Fig. 4). The link between maternal foraging time and time spent in large groups appeared to be weaker during age class 1 than in other age classes (Fig. 4).

Predictors of calf time in large groups during separations

During separations, the proportion of time that calves spent in large groups was related to calf age and the interaction between calf sex and the proportion of time spent in large groups while with the mother (Table 9). Calves tended to decrease the proportion of time in large groups with age (independent t tests: age class 1 versus 3, $t_{83} = 1.70$, $P = 0.09$; age class 1 versus 4, $t_{90} = 1.70$, $P = 0.09$; Fig. 5). The relationship between time spent in large groups during separations and time spent in large groups when with their mothers differed for male and female calves (Fig. 6). Female calves that spent relatively little time in large groups when with their mothers, also spent relatively little time in large groups during
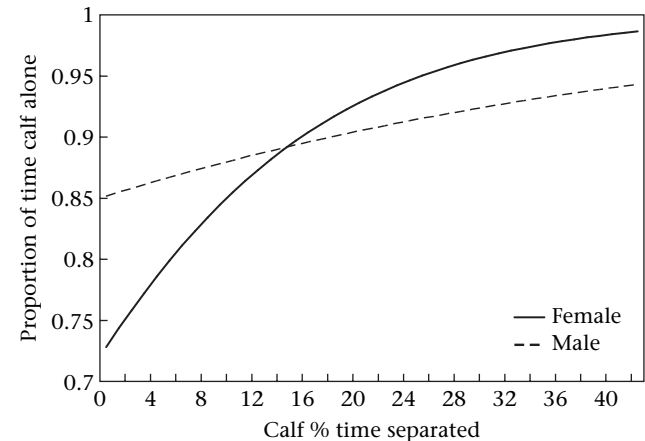

Figure 1. The interaction between calf sex and calf age class on the proportion of time that calves spent alone during separations. Adjusted means were calculated for each sex and age class combination, with calf hours observed (6.45 h), maternal foraging time (31.68%), calf percentage of time separated (18.70%) and the proportion of time that mother−calf pairs spent alone (0.50) held constant at their respective means.

Figure 2. The interaction between calf sex and calf percentage of time separated on the predicted proportion of time that calves spent alone during separations. Partial regression equations were calculated for each sex, with calf hours observed (6.45 h), maternal foraging time (31.68%) and the proportion of time that mother−calf pairs spent alone (0.50) held constant at their respective means. The maximum value on the X-axis scale was set at the 90th percentile.
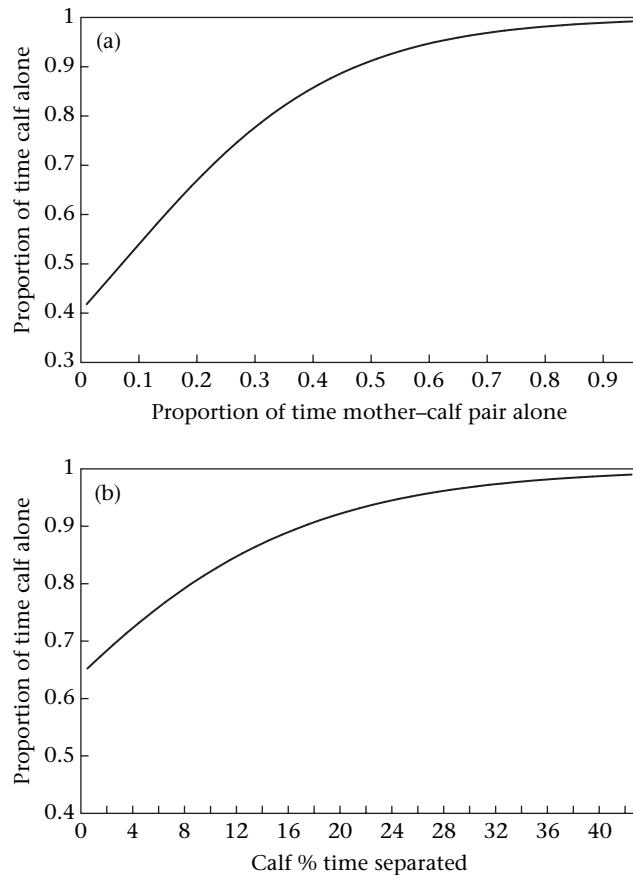
Figure 3. The interaction between (a) the proportion of time that the mother–calf pair were alone and (b) calf percentage of time separated on the predicted proportion of time that calves spent alone during separations. Partial regression equations were calculated for each sex, with calf hours observed (6.45 h), maternal foraging time (31.68%) and either the proportion of time mother–calf pairs spent alone (50.48%) or calf percentage of time separated (18.70%) held constant at their respective means. The maximum values on the X-axis scales were set at the 90th percentile.

separations. In contrast, male calves that spent relatively little time in large groups when with their mothers spent more time in large groups when separated.

The Composition of Calf Groups

Based on the average age–sex composition of the population, there did not appear to be a marked sex bias in availability of social partners (Fig. 7). However, mothers and calves did show preferences for some age–sex classes and avoidance of others. Calf groups contained a greater proportion of females, of all age classes, than was expected based on their availability (independent t tests: calves, $t_{51} = -23.94$, $P < 0.001$; juveniles, $t_{41} = -27.65$, $P < 0.001$; adults, $t_{13} = -24.34$, $P < 0.001$; Fig. 7). Male calves also comprised a larger proportion of calf groups than was expected (independent t test: $t_{15} = -4.29$, $P < 0.001$). In contrast, the proportion of juvenile males and adult males in calf groups was much lower than expected based on their representation in the population

Table 7. Results from the repeated measures ANOVA for the proportion of time that mother–calf pairs spent in large groups

Independent variable	df	F	P
Calf sex	2, 97	1.95	0.1479
Calf age	3, 141	2.28	0.0823
Maternal foraging time	1, 137	26.42	**<0.0001**
Calf hours observed	1, 148	1.4	0.2387
Calf sex×age	6, 129	1.2	0.3107
Maternal foraging×sex	2, 147	1.7	0.1858
Maternal foraging×age	3, 131	3.22	**0.0251**

Mother–calf pairs were considered to be in large groups if there were at least five other dolphins in addition to the mother and calf in the group. 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 ($P \leq 0.05$) are presented in bold.

(independent t tests: juveniles, $t_{10} = 22.68$, $P < 0.001$; adults, $t_{15} = 69.39$, $P < 0.001$; Fig. 7). In summary, mothers and calves preferentially associated with females of all ages and with male calves, but avoided juvenile and adult males.

Proportion of adults in calf groups

The proportion of adult females in calf groups was related to the interaction between calf sex and calf age class, as well as the interaction between calf sex and maternal presence–absence (Table 10). Both female and male calves had a higher proportion of adult females in their groups when together with their mothers ($\overline{X}_{female} = 36.73 \pm 2.84\%$; $\overline{X}_{male} = 41.76 \pm 3.40\%$) than during separations ($\overline{X}_{female} = 21.33 \pm 3.17\%$; $\overline{X}_{male} = 17.83 \pm 3.02\%$) (independent t test: female calves, together versus separate, $t_{126} = -5.09$, $P < 0.0001$; male calves, together versus
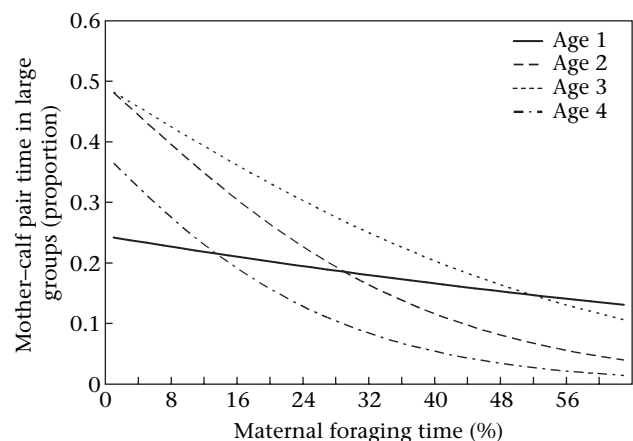

Figure 4. The interaction between calf age class and maternal foraging time on the predicted proportion of time that mother–calf pairs spent in large groups. Mother–calf pairs were considered to be in large groups if there were at least five other dolphins in addition to the mother and calf in the group. Partial regression equations were calculated for each age class, with calf hours observed (6.13 h) held constant at its mean. The maximum value on the X-axis scale was set at the 90th percentile. See Table 6 for significance of age class comparisons.

Table 8. Proportion of time that mother–calf pairs spent in large groups: maternal foraging time × calf age class

Age class comparison	Maternal foraging time		
	Low (10%)	Moderate (31%)	High (53%)
1 vs 2	0.0720	0.7300	0.0611
1 vs 3	**0.0195**	0.1626	0.9219
1 vs 4	0.8274	0.1304	**0.0332**
2 vs 3	0.6176	0.1174	0.1090
2 vs 4	0.2846	0.1998	0.3003
3 vs 4	0.1567	**0.0287**	**0.0397**

P values are presented for each age class comparison at the three levels of maternal foraging time that correspond with the mean ± 1 SD. Significant values ($P \leq 0.05$) are presented in bold. To control for variation in calf hours observed, this covariate was held constant at its mean (6.13 h) for these comparisons. Mother–calf pairs were considered to be in large groups if there were at least five other dolphins in addition to the mother and calf in the group.

separate, $t_{128} = -7.52$, $P < 0.0001$). In age class 1, we could not rule out a sex difference in which a higher proportion of adult females associated with mother–daughter pairs than mother–son pairs (independent t test: $t_{149} = 1.63$, $P = 0.106$). The proportion of adult females associated with mother–daughter pairs also decreased as calf age class increased from 1 to 3 (independent t test: female calves, age class 1 versus 3, $t_{144} = 2.78$, $P < 0.01$). However, the proportion of adult females in association with both mother–daughter and mother–son pairs tended to increase from age class 3 to age class 4 (independent t test: female calves, age class 3 versus 4, $t_{153} = -1.87$, $P = 0.0637$; male calves, age class 3 versus 4, $t_{170} = -1.83$, $P = 0.0691$).

Calf sex and age class both interacted with maternal presence–absence to affect the proportion of adult males in calf groups (Table 10). In age classes 1 and 3, calves had a higher proportion of adult males in their groups when

Table 9. Results from the repeated measures ANOVA for the proportion of time that calves spent in large groups during separations from their mothers

Independent variable	df	F	P
Calf sex	1, 123	1.72	0.1920
Calf age	3, 86	7.61	**0.0001**
Maternal foraging time	1, 124	0.37	0.5463
Calf hours observed	1, 120	1.55	0.2151
Calf % time separated	1, 122	0.65	0.4225
% Time in large groups 'together'	1, 120	0.00	0.9921
Calf sex×age	3, 86	1.18	0.3206
Calf hours observed×sex	1, 118	6.21	**0.0141**
% Time separated×sex	1, 122	2.65	0.1059
% Time in large groups 'together'×sex	1, 124	5.32	**0.0228**
Hours observed×% time in large groups 'together'	1, 114	3.37	0.0692

Calves were considered to be in large groups if there were at least two other dolphins (in addition to the calf) in the group. 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 ($P \leq 0.05$) are presented in bold.
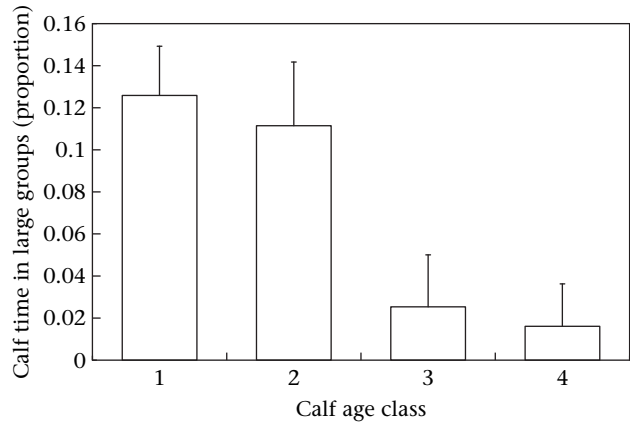

Figure 5. The relationship between calf age class and the proportion of time that calves spent in large groups during separations. Means are presented with standard error bars. Calves were considered to be in large groups if there were at least two other dolphins (in addition to the calf) in the group. Adjusted means were calculated for each age class, with calf hours observed (6.45 h), maternal foraging time (31.68%), calf percentage of time separated (18.70%) and the proportion of time that mother–calf pairs spent in large groups (21.09%) held constant at their respective means.

they were with their mothers than when they were separated from their mothers (independent t test: age class 1, together versus separate, $t_{142} = -3.78$, $P < 0.001$; age class 3, together versus separate, $t_{143} = -3.06$, $P < 0.01$). When calves were with their mothers, calf groups contained the highest proportion of adult males for age class 3. When separated from their mothers, calf groups contained the lowest proportion of adult males for age class 1. Female
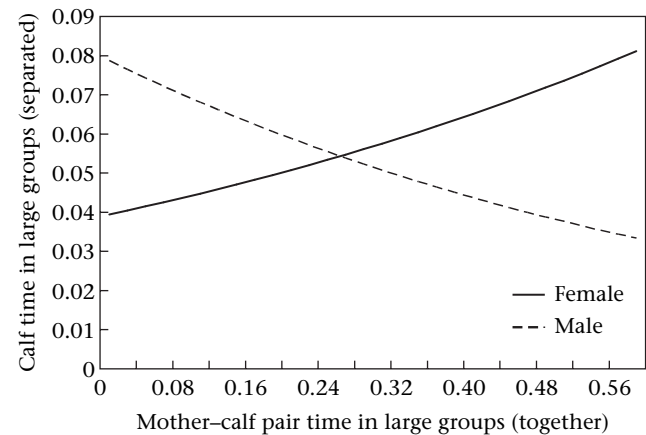

Figure 6. The interaction between calf sex and the proportion of time that mother–calf pairs spent in large groups on the predicted proportion of time calves spent in large groups during separations. Calves were considered to be in large groups if there were at least two other dolphins (in addition to the calf) in the group. Mother–calf pairs were considered to be in large groups if there were at least five other dolphins (in addition to the mother and calf) in the group. Partial regression equations were calculated for each sex, with calf hours observed (6.45 h), maternal foraging time (31.68%) and calf percentage of time separated (18.70%) held constant at their respective means. The maximum value on the X-axis scale was set at the 90th percentile.
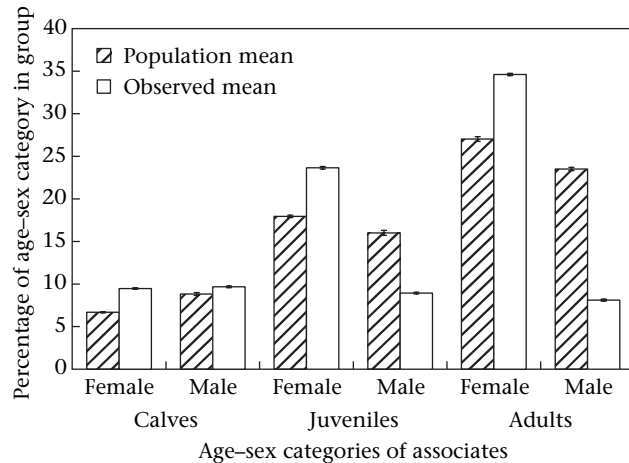
Figure 7. Calves' age- and sex-specific preferences for associates. Bars represent the average proportion of each age−sex category in the population and in observed calf groups.
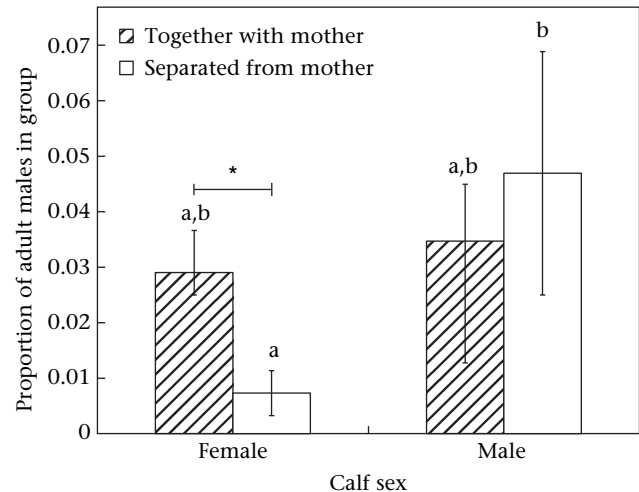

Figure 8. The interaction between calf sex and maternal presence−absence on the proportion of adult males in calf groups. An asterisk denotes significant differences ($P < 0.01$ within sexes). Different letters denote significant differences ($P < 0.01$ between sexes).

calves had higher proportions of adult males in their groups when with their mothers than when separated (independent t test: together versus separate, $t_{141} = -2.79$, $P < 0.01$; Fig. 8). This was not true for male calves. During separations, male calves had higher proportions of adult males in their groups than did female calves (independent t test: male calves versus female calves, $t_{205} = -2.79$, $P < 0.01$; Fig. 8).

Proportion of juveniles in calf groups

None of the factors that we examined (calf age class, calf sex and maternal presence−absence) were related to the proportion of juvenile females in calf groups (Table 10). However, calf age class and maternal presence−absence interacted to influence the proportion of juvenile males in calf

groups (Table 10). In age classes 2−4, juvenile males made up a larger proportion of calf groups during separations than while calves were with their mothers (independent t test: age class 2, together versus separate, $t_{160} = 2.19$, $P < 0.05$; age class 3, together versus separate, $t_{157} = 2.73$, $P < 0.01$; age class 4, together versus separate, $t_{160} = 3.15$, $P < 0.01$). When with their mothers, calves spent proportionately less time from age class 3 to age class 4 with juvenile males (independent t test: age class 3 versus 4, $t_{269} = 2.03$, $P < 0.05$). During separations, the proportion of juvenile males in calf groups increased as calves aged from age class 1 to age class 3 (independent t test: age class 1 versus 3, $t_{243} = -3.65$, $P < 0.001$).

Table 10. Repeated measures ANOVA table for the proportion of each age−sex class in calf groups

Independent variable	Adults			Juveniles			Calves		
	df	F	P	df	F	P	df	F	P
Females									
Calf sex	2, 169	3.81	**0.0242**	1, 119	1.42	0.2364	1, 108	0.59	0.4440
Calf age class	4, 228	3.40	**0.0101**	4, 177	0.56	0.6918	4, 180	2.47	**0.0462**
Maternal presence−absence	1, 128	24.90	**<0.0001**	1, 109	0.04	0.8444	1, 123	1.59	0.2097
Calf sex×calf age class	8, 146	2.40	**0.0182**	4, 102	1.04	0.3894	4, 115	2.02	0.0968
Calf sex×maternal presence−absence	2, 132	7.67	**0.0007**	1, 114	0.18	0.6682	1, 129	3.75	0.0551
Calf age class×maternal presence−absence	4, 128	0.32	0.8630	4, 112	0.99	0.4137	4, 127	2.68	**0.0344**
Males									
Calf sex	1, 134	4.66	**0.0327**	2, 175	0.42	0.6572	1, 89	0.25	0.6153
Calf age class	4, 191	1.76	0.1384	4, 239	2.09	0.0831	4, 144	1.01	0.4018
Maternal presence−absence	1, 141	2.30	0.1318	1, 158	0.81	0.3685	1, 115	11.03	**0.0012**
Calf sex×calf age class	4, 120	1.07	0.3734	8, 177	0.59	0.7877	4, 112	0.59	0.6710
Calf sex×maternal presence−absence	1, 143	9.01	**0.0032**	2, 159	1.72	0.1822	1, 121	2.98	0.0868
Calf age class×maternal presence−absence	4, 143	3.31	**0.0126**	4, 158	6.00	**0.0002**	4, 120	0.55	0.6979

Calves of unknown sex were excluded from all analyses, except those for adult females and juvenile males, because of an inability to achieve model convergence with them included. The analyses for adult females and juvenile males were conducted using all available calves (female, male and unknown sex). The variable maternal presence−absence refers to whether the calf was together with its mother or temporarily separated from her. Significant values ($P \leq 0.05$) are presented in bold.

Proportion of calves in calf groups

Calf sex and age interacted with maternal presence–absence to predict the proportion of female calves in calf groups (Table 10). The interaction between calf sex and calf age class was marginally nonsignificant (Table 10). Both female and male calves showed a general pattern of decreasing the proportion of female calves in their groups as they aged, but this pattern was strong for male calves and weak for female calves. The decrease was marginally nonsignificant for female calves between age classes 1 and 2 (independent t test: age class 1 versus 2, $t_{111} = 1.93$, $P = 0.056$). Male calves significantly decreased association with female calves from age class 2 to age class 3 (independent t test: age class 2 versus 3, $t_{125} = 2.49$, $P = 0.01$). In age class 2, male calves associated with more female calves than female calves did (independent t test: female calves versus male calves, $t_{134} = -2.36$, $P = 0.02$). Female calf groups contained more female calves when calves were separated from the mother than when calves were with the mother (independent t test: together versus separate, $t_{124} = 1.97$, $P = 0.05$). When together, mother–son pairs tended to have more female calves in their groups than did mother–daughter pairs (independent t test: female calves versus male calves, $t_{87} = -1.65$, $P = 0.10$). Within age classes, the only significant difference between calf groups when with the mother and when separated occurred in age class 1, where there were more female calves in groups during separations (independent t test: together versus separate, $t_{129} = 5.38$, $P < 0.0001$). During separations, the proportion of female calves in calf groups decreased as calves aged from age class 1 to age class 4 (independent t test: age class 1 versus 2, $t_{209} = 1.83$, $P = 0.07$; age class 1 versus 3, $t_{230} = 2.57$, $P = 0.01$; age class 1 versus 4, $t_{220} = 2.73$, $P < 0.01$).

The proportion of male calves in calf groups was marginally related to the interaction between calf sex and maternal presence–absence ($P = 0.09$; Table 10). Despite the fact that only female calves increased their association with female calves during separations, calves of both sexes increased their association with male calves during separations (independent t test: female calves, together versus separate, $t_{115} = 2.54$, $P = 0.01$; male calves, together versus separate, $t_{116} = 3.66$, $P < 0.001$; Fig. 9). However, there were no sex differences in association with male calves within the 'together' or 'separated' category.

DISCUSSION

Summary of Main Findings

Our group size analyses indicated several main trends. First, when mother–calf pairs were together, maternal foraging time was a strong predictor of group size. As maternal foraging time increased, mother–calf pairs increased their proportion of time spent without additional associates ('alone') and decreased the proportion of time spent in large groups. Second, during separations from their mothers, calf age was a main predictor of group
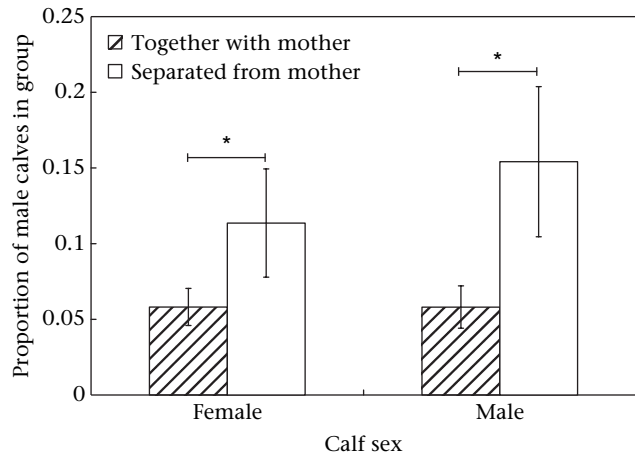

Figure 9. The interaction between calf sex and maternal presence–absence on the proportion of male calves in calf groups. Symbol designations as in Fig. 8.

size. In general, as calves increased in age they spent more time alone and less time in large groups. However, this pattern was stronger in female calves than male calves. And finally, although calves of both sexes maintained consistency in their time alone when with their mothers and when separated from them, calves showed a striking sex difference in the relationship between time spent in large groups when with their mothers and when separated. While female calves appeared to mirror the group size patterns of their mothers when separated, the group size patterns of male calves during separations were opposite to those when they were with their mothers.

A group composition analyses also yielded several main patterns. In general, calves had a higher proportion of adults (female and male) in their groups when together with their mothers than when separated. In contrast, the proportion of immatures (juvenile males, female and male calves) in calf groups was higher when calves were separated from their mothers than when they were with their mothers. During separations, calf age was also a predictor of group composition. As calves of both sexes increased in age, the proportion of juvenile males in their groups increased while the proportion of female calves decreased.

Despite the attention that has been given to the complex nature of fission–fusion society in bottlenose dolphins (e.g. Connor et al. 1999, 2000, 2001; Lusseau 2003; Wells 2003; Lusseau & Newman 2004), little attention has been paid to how and when social patterns form. Our analyses of group size and composition from a calf's perspective provide the first analyses of factors related to the development of these social patterns in bottlenose dolphins. Also, although a number of studies report sex biases in dyadic association (e.g. Wells et al. 1987; Smolker et al. 1992), this is the first report of the age and sex composition of dolphin groups.

Predictors of Calf Group Size

Group size is a major component of social organization, and probably the most often examined. The average

reported group size for bottlenose dolphins in Shark Bay is 4.8 overall (Smolker et al. 1992) and 5.9 specifically for adult females (Mann et al. 2000). In this study, the mean group size for calves was 4.3 dolphins (including calf and mother) and the range for all calf groups was 0–19 associates. Thus, the mean group size of calves appears to be on par with that of the overall population, but slightly lower than that previously reported for adult females (including mothers). This difference may be due to sampling differences where solitary individuals are more likely to be captured in focal than survey data (Q. Gibson & J. Mann, unpublished data). However, group size is highly variable and it seems unlikely that the optimal group size for mothers with dependent calves would match that of the overall population. Based on our finding that mothers and calves spent $51.31 \pm 3.21\%$ of their time alone, and given the energetic demands of lactation (e.g. Cheal & Gales 1991), and that maternal foraging time was correlated with the proportion of time spent alone, it is clear that lactating females spend considerable periods of time alone to forage (see Mann & Watson-Capps 2005). Therefore, our examination of the proportion of time that mothers and calves spent in groups of various sizes may provide more insight into the function(s) of calf groups.

Maternal characteristics

One of our main findings was that maternal sociality predicted calf sociality. Both male and female calves that spent a large amount of time alone with their mothers also spent a relatively large amount of time alone during separations. However, the sociability of daughters and sons differed depending on how sociable the mother was in terms of group size. Daughters, again, mirrored the mother, but sons did the opposite of their mother, seeking fewer associates if the mother was sociable, and seeking more if the mother was less sociable. One possible explanation is that sons of social mothers have more social opportunities than sons of solitary mothers and probably use their time separated from their mothers to forage. In contrast, male calves that spend relatively little time in large groups when with their mothers may be at a disadvantage and may make more of an effort to join others during separations; they probably have numerous foraging opportunities while with their relatively asocial mothers. If daughters adopt the socioecological strategies of their mothers, then they emulate them from an early age.

Because foraging is a predominantly solitary activity in Shark Bay (Mann & Sargeant 2003; Mann & Watson-Capps 2005), we expected maternal foraging time to be inversely related to mother–calf sociality. When calves were with their mothers, maternal foraging time was positively correlated with the proportion of time that calves spent alone and negatively correlated with the proportion of time that calves spent in large groups. Maternal foraging time was not expected to directly affect calf sociality during separations, yet during age classes 2 and 4, increased maternal foraging time resulted in decreased time in solitary separations. Mother–calf pairs are most sociable (highest percentage of time in large groups) in age classes 1 and 3, first after the birth of a calf and then again when a mother

is attractive to males (mother–calf groups contained the highest proportion of adult males during age class 3; see below). Thus, this pattern suggests that calves with predominantly solitary mothers (i.e. those that spend a large amount of time foraging) may compensate by seeking out associates during separations in age classes 2 and 4, when their mothers tend to be least sociable.

Calf characteristics

With age, calves of both sexes spent more time on solitary separations and less time in large groups, but this pattern was stronger for female than male calves. During separations, both male and female calves spent more time alone in age class 4 than in age class 1, but female calves also spent more time alone in age class 3 than age classes 2 and 1. There was also a tendency for calves to spend more time in large groups during separations when young (age classes 1 and 2) than when older (age classes 3 and 4). However, these large groups may function to provide more socializing opportunities rather than protection (see below).

Variation in calf independence was related to sociality. Highly independent calves (i.e. those that spent more time separated) spent proportionately more time alone during separations than did less independent calves. This pattern suggests that highly independent calves devoted more time to solitary activities such as foraging. This idea is supported by our finding that at high (34%) levels of separation, female calves spent more time alone than male calves. This sex difference was expected since previous analyses have indicated that female calves spend more time foraging during far separations than do males (Gibson & Mann 2008).

Calf Group Composition

Based on the relative availability of calf, juvenile and adult males and females in the population, mothers and calves appear to avoid juvenile and adult males and prefer to associate with calves of both sexes and juvenile and adult females. As with most mammals, male bottlenose dolphins are more aggressive than females, even as calves when aggression rates are lowest (Scott et al. 2005). Thus, we expected mothers and calves to avoid associating with juvenile and adult males, except when mothers were cycling and might not be able to avoid them. Alternatively, adult males may find mother–calf groups less attractive, except when the mother is fertile. Associations with male juveniles and calves were more common during mother–calf separations, especially among male calves, possibly in support of the same-sex bonds and/or social skills hypotheses (see also Mann 2006).

Maternal presence–absence effects

Calf association with every age–sex class, except juvenile females, differed depending on whether the calf was with its mother or separated from her. Calf groups contained a smaller proportion of adult females during separations than when calves were with their mothers, indicating that association between adult females and

mother−calf pairs is primarily driven by a relationship with the mother and not an interest in the calf.

Similarly, adult males associated with mother−calf groups because of their interest in mothers, not calves. This pattern was more evident in female calf groups. However, in age classes 1 and 3, the proportion of adult males in calf groups was higher when calves (of both sexes) were with their mothers than when mothers and calves were separated. Calves are likely to encounter more adult males during age class 3 because of increased male interest in the mother as the calf approaches weaning, but overall levels of association between adult males and mother−calf pairs were relatively low.

Interestingly, association with juvenile females did not vary with calf sex, age or maternal presence−absence. Juvenile females are a stable presence in the social lives of calves, but show no preference for associating with calves over mothers. An exception might occur with newborn calves, to which nulliparous females are attracted (Mann & Smuts 1998). In contrast, calf groups (except in age classes 0 and 1) contained a greater proportion of juvenile males during separations than when calves were with their mothers. This is surprising considering the higher rates of aggression in juvenile males (Scott et al. 2005), yet it may indicate that calves are more tolerant of (and perhaps even interested in) rough socializing than their mothers; calves also receive little aggression compared to their mothers (Scott et al. 2005). Male calves, in particular, may seek out interactions with juvenile males (Mann 2006). Alternatively or additionally, mothers might avoid juvenile sons, a pattern expected given bisexual philopatry. Calves might only be able to join up with male kin during separations.

Although calves of both sexes spent more time with male calves during separations, only female calves increased time spent with other female calves during separations. However, despite the apparent sex-biased increase in association with female calves, male and female calf groups contained essentially equal proportions of female calves during separations.

Calf characteristics

Although there was no strong evidence in support of a same-sex bias, our results do suggest that calves prefer immatures (calves of both sexes and male juveniles) to adults. Calf groups contained lower proportions of adults (both female and male) and higher proportions of male juveniles and calves (of both sexes) when calves were separated and associating independently of their mothers than when claves were with their mothers. Adult females may be less interested in associating with calves and vice versa. When with their mothers, calves spent most of their social time with other adult females, presumably their mothers' preferred associates. During separations, calves have an opportunity to socialize with immatures of both sexes, as evidenced by the increased proportion of male and female calves in calf groups during separations. But surprisingly, both male and female calves decreased their association with female calves as they aged. This finding suggests that female calves are either less attractive social partners than male calves, female calves are less interested

in social activities as they age, or both. Data on female calf foraging (Gibson & Mann 2008) and our finding that female calves engage in more solitary separations suggest that female calves' interest in social activities decreases with age.

Possible Functions of Calf Groups

Maternal influence

The maternal influence hypothesis was largely supported by our finding that calf sociality was predicted by maternal sociality; this relationship was stronger for daughters than sons. Given what we know about the transmission of foraging tactics (Mann & Sargeant 2003) and female kinship bonds (Möller et al. 2006), this pattern was expected. Daughters adopt the socioecological strategies of their mothers. These early sex differences are similar to those observed in other mammals. In ungulates with male biased dispersal, male calves tend to show less connection to their mothers by increasing their average distance (e.g. giraffes, *Giraffa camelopardalis*: Pratt & Anderson 1979) or decreasing their rates of interaction with their mothers (e.g. elephants, *Loxodonta africana*: Lee 1986) as they mature, while female calves keep their interaction rates nearly constant. In some cases (e.g. reindeer), males consistently stray further from their mothers than do female calves throughout development (Mathisen et al. 2003). Thus, maternal sociality is likely to have a stronger influence on the social patterns of daughters than on those of sons in these mammals as well. But unlike other mammals where the general patterns is for all male offspring to distance themselves from their mothers, male dolphin calves appear to adjust their social patterns in response to how much social experience they obtain while with their mothers. This difference may potentially be explained by the highly variable nature of early social experiences for bottlenose dolphin calves and the dramatic decrease in association between mothers and sons (averaging less than 1%) postweaning (J. Mann, unpublished data). Therefore, the social pressures for male dolphin calves may be greater and occur at an earlier age than those for female offspring.

Our third prediction, that the proportions of each age−sex class in calf groups during separations would be similar to those when with the mother, was not supported by our data. Juvenile females were the only exception. Therefore, even though male and especially female calves are similar to their mothers in terms of their degree of sociality, they differ in who they preferentially associate with.

Same-sex bonds

There was some support for the same-sex bonds hypothesis in that male calves had higher proportions of same-sex immatures (male juveniles and calves) in their groups when they were separated from their mothers than when they were with their mothers. Female calves also had higher proportions of female calves in their groups when they were separated from their mothers than when they were with their mothers, but the proportion of

juvenile females was the same regardless of maternal presence. We also predicted an increase in the proportion of same-sex associates with age, but only found an increase in male calf association with juvenile males, and not other male calves, with age. Female calves did not change who they preferentially associated with (age–sex class).

Because of the sex-biased natal dispersal characteristic of most mammals, long-term bond formation during the infant and juvenile periods is typically limited to the nondispersing sex (usually females), except when peers emigrate from their natal groups together (e.g. vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1983; longtailed macaques, *Macaca fascicularis*: van Noordwijk & van Schaik 1985; African lions, *Panthera leo*: Pusey & Packer 1987). However, natal philopatry by both sexes in bottlenose dolphins (Connor et al. 2000) renders long-term, multigenerational bonds within and between males and females possible. Our data lend some support to the notion that the early association patterns of dolphin calves enable long-term relationships to form. Both sexes showed same-sex preferences in association. To better test this hypothesis, we need to track dyadic and potentially polyadic association patterns from infancy to adulthood.

Protection

Two group size predictions for the protection hypothesis were supported by our data. Young calves, because of their small size, lesser defences and greater mortality risk, are more vulnerable to predation than are adults. As expected, calves spent more time on solitary separations and less time in large groups as they aged. However, this pattern was stronger for female calves than for male calves, possibly because other factors influence group size at older ages. Furthermore, although there was a tendency for calves to be in larger groups when they were younger, these large groups may provide more socializing opportunities than they do protection. Previous analyses have shown that calf socializing peaks during age class 1 and decreases with calf age (Gibson & Mann 2008). In addition, calves were expected to associate with a similar or higher proportion of juvenile and/or adult females during separations compared to when they were with their mothers because these individuals are more likely to offer protection. While juvenile female–calf association was not related to maternal presence, calf association with adult females decreased during separations. In addition, mothers and calves spent substantial amounts of time alone (54%) and most calf separations were solitary. Although separation from the mother probably entails higher predation risk, separation rate does not change with season or level of predation risk, (Mann & Watson-Capps 2005). Calves separate from their mothers most often when the mother is foraging (Mann & Watson-Capps 2005), perhaps because they cannot keep up during extended maternal foraging bouts, they hinder the mother, and/or they take advantage of these bouts to hunt for themselves or socialize. Calves may gain some protective benefit from association with other calves or immatures during separations by dilution, detection or deterrence, even if defence is unlikely. Several

ungulate species, such as giraffes, leave their calves in crèches rather than alone (Pratt & Anderson 1979), and this pattern is thought to offer greater protection (selfish herd hypothesis). Although dolphin mothers do not cache their offspring, calves may reduce their risk of predation by occasionally grouping while their mothers forage. Even if calves group with each other to gain social skills, reduced predation risk may be a beneficial by-product. Alternatively, some ungulate calves seek out social opportunities even if these social opportunities result in increased predation risk (e.g. greater distance from mother and higher activity levels) because these social behaviours may enhance later reproductive success via skill development (e.g. fighting ability: Mathisen et al. 2003). Although larger group sizes might afford protection from predation for young dolphin calves, consistent with previous studies (Mann & Watson-Capps 2005), predation pressure does not appear to have an overwhelming influence on calf social patterns.

If calf groups provide protection from conspecific aggression, calves would be less likely to associate with juvenile and adult males overall (generally true), and during separations. This prediction received only partial support. Calves associated less with adult males during separations than when they were with their mothers, possibly because association with adult males is risky, adult males have no interest in associating with calves, or both. But in contrast to our prediction, calves increased the proportion of male juveniles in their groups during separations in age classes 2–4, but not in age class 1. This pattern provides more support for the social skills hypothesis than for the protection hypothesis (see below).

Social skills

All three of our group size and composition predictions for the social skills hypothesis were supported, particularly for males. Males with less gregarious mothers appeared to compensate by seeking out social opportunities during separations. Calves of both sexes also preferentially associated with calves and male juveniles during separations. Male juveniles and calves may be more willing and challenging partners than female juveniles, and/or mothers may be less tolerant of juvenile males than they are of juvenile females.

Play behaviour enables immature individuals to develop skills that will be used throughout their lives. Social play, in particular, is often similar in nature to conflicts among adults in that these types of interactions involve rapid decision making in response to the behaviour of others and the ability to predict how others will respond to one's own actions (Fairbanks 2000). Therefore, this type of play promotes the physical and cognitive development necessary for similar adult activities (Fairbanks 2000). Play in most mammals is biased towards peers and occurs more often and more aggressively among males (reviewed in Byers 1984; Meaney et al. 1985). Therefore, it is not surprising that the calves in our study increased their association with other immatures, particularly those of the same sex, when separated from their mothers. Furthermore, sex differences in mammalian social play often foreshadow differences in adult behaviour. In bottlenose dolphins,

social skill development is likely to take priority over foraging skill development for male calves, whereas the reverse is probably true for female calves. The sociosexual interactions of male calves resemble adult male alliance and consort behaviour (Mann 2006). In humans, there is some indication that sexually segregated socialization is self-mediated; children tend to associate in same-sex groups (reviewed in Maccoby 2002). As in other mammals, play among boys is more physical and aggressive and tends to occur in larger groups than that among girls (reviewed in Maccoby 2002). These patterns suggest that same-sex peers play a primary role in shaping early social patterns. Such self-socialization may be particularly prevalent among bottlenose dolphin calves because of their ability to choose which individuals to associate with (or avoid) when interacting independently of their mothers.

Conclusion

Although we found some support for all of the functional hypotheses for calf groups, the social skills hypothesis was best supported by our data for male calves and moderately for female calves. The maternal influence hypothesis was also supported for both sexes, but strikingly so for daughters. While mothers show clear same-sex preferences, the same was not strictly true for their calves. By preferentially associating with immatures, and males in particular, calves may gain considerable social experience. Some long-term, same-sex bonds are probably initiated in the first few years, but can be better documented by tracking these relationships over time. With age, female calves show less interest in social interactions and greater interest in foraging during separations (Gibson & Mann 2008). Thus, calves adjust their social patterns during separations to reflect their underlying sex-specific fitness interests. That female calves model their behaviour more closely to their mothers is another indication. Temporary mother–calf separations may serve a similar function to the larger fission–fusion social system in that mothers and calves are able to structure their group size and composition to maximize the benefits at a specific point in time. Bottlenose dolphin calves are faced with a number of social and ecological challenges before they are weaned. We suggest that calves play an active role in meeting these sex-specific challenges by patterning their behaviour during separations according to the experiences they are afforded while with their mothers.

Acknowledgments

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