

## Do sampling method and sample size affect basic measures of dolphin sociality?

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### ABSTRACT

Although the fission–fusion social patterns of bottlenose dolphins have been described, defining and measuring sociality is difficult. No study to date has investigated *how much* data are necessary to accurately depict social patterns in a fission–fusion species and whether this amount differs depending on the measure used. Using the long-term Shark Bay bottlenose dolphin study we examined four different measures of sociality for mothers and dependent calves ( $n = 89$ ). Our objectives were to determine (1) the amount of observation time necessary to accurately depict sociality using these measures, (2) correlations among these measures, and (3) if sampling method affects the validity of sociality measurements. A minimum of 10 h and 5 h of observations, respectively, were necessary to accurately capture calf associate numbers and percent time alone. A pairwise comparison of calf sociality measurements from focal and survey data found that calves spent from 0% to 70.2% of their time alone in focal data, but these same calves spent only 0%–7.7% alone in survey data. These findings indicate that (1) results differ depending on the type of sampling method and (2) the amount of observation time necessary to adequately capture individual variation differs depending on the measure of sociality.

Key words: sociality, fission–fusion, bottlenose dolphin, *Tursiops* spp., association, group size.

Everywhere they have been studied, bottlenose dolphins (*Tursiops* spp.) live in complex fission–fusion societies characterized by frequent changes in subgroup size and composition (reviewed in Connor *et al.* 2000). Yet despite this fluidity, individuals form long-lasting, individually specific association preferences (*e.g.*, male alliances, Connor *et al.* 1992; female kin, Möller *et al.* 2006) and females vary greatly in their degree of sociality (Smolker *et al.* 1992). Although the association patterns of this species have been described in some detail (*e.g.*, Wells *et al.* 1987, Smolker *et al.* 1992, Gero *et al.* 2005, Lusseau *et al.* 2006, Möller *et al.* 2006), defining and measuring sociality is difficult when group size and composition are temporally variable.

Association indices, such as the halfweight index (Cairns and Schwager 1987), which measure association between pairs of individuals, have become the primary method for describing social patterns in delphinids (*e.g.*, Wells *et al.* 1987, Smolker *et al.* 1992, Slooten *et al.* 1993, Herzing and Brunnick 1997, Bejder *et al.* 1998, Quintana-Rizzo and Wells 2001, Owen *et al.* 2002, Grellier *et al.* 2003, Rogers *et al.* 2004, Karczmarski *et al.* 2005, Lusseau *et al.* 2006, Möller *et al.* 2006). However, more recently developed analytical techniques are also being used to describe the temporal and spatial stability of associations (*e.g.*, lagged association rates, Whitehead 1995, Owen *et al.* 2002, Karczmarski *et al.* 2005), as well as the structure of dolphin social networks (Lusseau *et al.* 2006).

The questions of (1) how to define social groups and (2) which aspects of sociality (*e.g.*, group size, composition, number of associates, *etc.*) to measure are not trivial ones. Group size is fundamental to theories of social evolution (*e.g.*, Sterck *et al.* 1997) and is probably the most often reported component of social organization. Although group size is relatively easy to measure, definitions and methods vary widely, even among those studying the same species or population. For example, criteria used to define bottlenose dolphin groups range from the conservative 10-m chain rule (*e.g.*, Smolker *et al.* 1992, Gero *et al.* 2005) to all dolphins within an approximate 100-m radius of the observer (Quintana-Rizzo and Wells 2001) to all individuals within sight moving in the same general direction, interacting or engaged in similar activities (Owen *et al.* 2002, Grellier *et al.* 2003, Rogers *et al.* 2004, Möller *et al.* 2006). Such differences hinder comparisons across sites but are not unique to dolphin studies. Fission–fusion societies are rare among mammals, and bottlenose dolphins are described as having fission–fusion social patterns most closely resembling those observed in chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles paniscus*) (Symington 1990, Smolker *et al.* 1992). The definition of group membership in chimpanzees and spider monkeys is similarly variable, ranging from a 50-m chain rule (Otali and Gilchrist 2006) to all independently feeding individuals (>5 yr of age) visible to the observer (Chapman *et al.* 1995, Lehmann and Boesch 2004) to all individuals within acoustic range (*i.e.*, seen within 1 h, Chapman *et al.* 1995). Thus, although the decision of how to define groups may be somewhat arbitrary, it clearly has ramifications for our ability to compare results from different studies.

Once “group” has been defined, a variety of social measures can be studied. For example, the total number of associates for each individual provides an estimate of the potential number of relationships maintained over time, whereas the frequency distribution of group size reflects how individuals distribute their associates in time. Other measures such as percent time socializing, percent time in groups, and its inverse, percent time alone, measure the degree of social stimulation, the nature of social relationships, and/or the social time budget. Yet another measure, the rate of fission–fusion, which has not yet been reported for bottlenose dolphins, indicates the temporal stability or fluidity of association. Analyses of each of these measures may provide valuable information about the fitness benefits and consequences of sociality, and thus contribute to theories of social evolution (*e.g.*, Sterck *et al.* 1997, Silk 2007). Furthermore, such measures have been used as proxies for social complexity in numerous comparative studies examining the apparent co-evolution of social complexity and brain size (*e.g.*, Dunbar 1992, Marino 1996, Joffe and Dunbar 1997, Barton 1998, Connor and Mann 2005). Although fission–fusion societies are often described as complex, behavioral complexity remains ill defined (Healy and Rowe 2007) and the social measures relevant for determining complexity are rarely reported. Thus, obtaining valid measurements of

sociality, using these measures or others, is critical to the theories that are based upon them.

No study to date has investigated how much data are necessary to accurately depict social patterns in a fission–fusion species and whether this amount differs depending on the measure used. Although photo-identification mark-recapture techniques have been used to determine when most of the individuals in a population were “captured” (*e.g.*, Durban and Parsons 2000, Karczmarski *et al.* 2005), this method has less descriptive value for assessing social patterns within a population. Therefore, this study used data from the long-term Shark Bay bottlenose dolphin mother–calf study to examine four different measures of sociality for mothers and dependent calves: number of associates, percent time in groups, percent time alone, and number of simultaneous companions. These basic measures of sociality are biologically significant, relating to calf survival, time budgets, social patterning (types of associates), maternal care, and calf developmental strategies (Mann and Watson-Capps 2005; Gibson and Mann 2008*a, b*). Our objectives were to determine (1) the amount of observation time necessary to accurately depict sociality using these measures, (2) correlations among these measures, and (3) whether the sampling method affects the validity of sociality measurements.

#### METHODS

This research was conducted in Shark Bay, Western Australia, and is part of the longitudinal mother–calf study that was initiated in 1988. Our study site encompasses an area of approximately 250 km<sup>2</sup> in the eastern gulf of Shark Bay, just offshore of Monkey Mia. In addition to collecting survey data (*i.e.*, sighting records) of groups since 1984, individual mothers and calves have been followed every year since 1988 (Mann and Watson-Capps 2005) using focal animal sampling techniques (Mann 1999). Our surveys are designed to collect brief sighting records for groups of dolphins using one-zero sampling, in which an observer records the presence or absence of an individual during a 5-min interval (see Mann 1999). In practice, this means repeated scanning of the group over 5 min to determine who was present during the first 5 min of the survey. Predominant activity is determined by scan sampling where the specific activity of each individual is noted at least once in the first 5 min. In contrast, our focal follows (Mann 1999) are conducted to collect detailed behavioral information (*e.g.*, group composition, activity, mother–calf proximity, social interactions, *etc.*) on specific mother–calf pairs using a combination of point (1-min intervals) and continuous sampling techniques (Altmann 1974).

For both types of data collection, associations were determined via a 10-m chain rule in which an individual was considered to be in the group if it was within 10 m of another individual in the group. Thus, mothers and calves were considered separated if they were greater than 10 m from each other with no other dolphins linking them. In focal data, group membership was recorded every minute. In contrast, all animals within a 10-m chain during the first 5 min of a survey were considered to be in a group. Individuals were identified visually or by photo-ID based on the distinctive characteristics (*e.g.*, size, shape, and markings) of their dorsal fins and body markings.

Our analyses included data on calves from birth until age 4, weaning, or death (whichever occurred first) that were observed in our focal study for at least 1 h in a single age-class. These criteria generated 1,165 focal hours of observation on 49 mothers and 89 calves ( $\bar{x} = 13.1 \pm 1.3$  h/calf, range = 1.0–50.7 h/calf). Of

these 89 calves, we restricted the sample to those sighted more than 10 times in our survey data for analyses comparing sampling methods. In addition, to reduce observer bias as a factor, we only used survey data collected by observers who also collected data for the mother–calf focal data set because they were skilled at calf identification. This reduced our sample size to 1,296 surveys on 45 calves ( $\bar{x} = 28.8 \pm 2.2$  surveys/sighting records per calf).

Each of our four sociality measures were calculated using focal follow data (see Gibson and Mann 2008*a, b*). Although most studies of bottlenose dolphin association use survey data, focal follow data offer numerous benefits when examining mother–calf association patterns. For instance, young calves are often less identifiable than older animals and in some cases the presence of its mother is necessary to positively identify a calf. Yet mother–calf pairs tend to spend substantial amounts of time alone and separate from each other frequently (Gibson and Mann 2008*a, b*). Thus, in surveys in which a mother and calf are separated, the calf may be misidentified or overlooked. In contrast, during focal follows we are able to stay with an individual calf during temporary mother–calf separations and quantify independent calf association patterns with a high level of precision.

Our first sociality measure, the number of associates, was determined by counting the number of unique, known individuals observed in association with either the mother or the calf. Although we excluded associates whose identity was unknown from the associate count, unknowns constituted only 2.5% of total associate data points (*e.g.*, number of minutes spent with unidentified individuals divided by the number of minutes spent with known individuals) and are not expected to affect our results. Because the number of associates is likely an underestimate, mothers' numbers of associates were cumulative across calves to more accurately reflect the number of lifetime associates. The number of calves' associates was cumulative across the calf period to demonstrate the number of associates early in life. Our second measure, the percent time mothers and calves spent in groups, was calculated as the number of minutes the mother or calf was observed in a group with at least one other dolphin besides the mother/calf divided by the total number of minutes they were observed. In other words, when a mother–calf pair was together but not in association with any other dolphins, neither the mother nor the calf was considered to be in a group. The third sociality measure, percent time alone, was calculated as the number of minutes the mother and calf were completely alone (*i.e.*, mother and calf were separated and not with any other dolphins) divided by the total number of minutes they were observed. Thus, based on our methods of calculation, percent time in groups and percent time alone are not true inverses of each other. And finally, our last sociality measure, the mean number of simultaneous companions, was only calculated for calves because we focused on associates available to calves. To clarify, the number of “simultaneous companions” refers to the number of individuals in addition to the mother and calf in the group. We excluded from our analyses data minutes in which group size was uncertain, except when it was known that at least seven individuals (in addition to the mother and calf) were present. These groups were included to prevent a bias against large groups since exact group size was more likely to be uncertain in larger than in smaller groups.

To determine the amount of data necessary to accurately assess sociality, we first plotted each of the four sociality measures *vs.* observation time to identify the approximate point at which the relationship leveled off. We then used this information to limit the data set to mothers/calves observed a minimum number of hours (based on the visually identified cutoff) and performed Spearman's rank correlations. If

the measure remained correlated to hours of observation, the data set was further restricted (by raising the minimum number of hours observed by one) and the correlation was reassessed. This process continued until the sociality measure and hours of observation were no longer correlated, thereby identifying the minimum number of observation hours for each sociality measure. The relationship between these sociality measures was also assessed using Spearman's rank correlations.

Finally, because both our focal data and survey data use virtually the same definition for group membership, we evaluated whether or not the use of survey data generated comparable results to our analyses with focal data. This is a question of external validity: Does the sampling method accurately capture patterns of sociality? To answer this question, we conducted a pairwise comparison of percent time alone calculated from focal and survey data. Since we were initially interested in whether or not calves were overlooked in survey data, we first selected the 10 most solitary calves from our focal data set and recalculated their percent time alone using survey data. This data set was not restricted to calves sighted in 10 or more surveys. We then repeated the comparison, using all calves in our restricted data set (*i.e.*, those observed in 10 or more surveys), for two measures of sociality: percent time alone and percent time in groups.

## RESULTS

### *Summary Statistics*

Based on focal data, individual variation among mothers and calves was large for all of the sociality measures examined (Gibson and Mann 2008*a, b*). The number of unique associates ranged from 0 to 139 for mothers (unadjusted for hours observed,  $\bar{x} \pm \text{SE} = 39.4 \pm 5.3$ ) and from 0 to 77 for calves (unadjusted for hours observed,  $\bar{x} = 27.6 \pm 2.2$ ). For our second measure, mothers and calves both ranged from 0 to 100% time spent in groups with others (mothers:  $\bar{x} = 44.9 \pm 4.3$ ; calves:  $\bar{x} = 46.8 \pm 3.0$ ). Percent time alone ranged from 0% to 71.3% for both mothers ( $\bar{x} = 13.4 \pm 2.1$ ) and calves ( $\bar{x} = 13.0 \pm 1.5$ ). Our final sociality measure, the mean number of simultaneous companions for calves, varied from 0 to 11 dolphins ( $\bar{x} = 2.3 \pm 0.4$ ; range for all groups = 0–19 dolphins).

### *Observation Time*

Of these sociality measures, the number of associates was correlated with the total focal observation time (Spearman's rank correlation:  $r_s = 0.571$ ,  $P < 0.001$ ,  $n = 89$ ); though limiting the data set to calves observed 10 or more hours rendered this correlation nonsignificant ( $r_s = 0.225$ ,  $P = 0.15$ ,  $n = 42$ ). In other words, for our data set we would need 10+ focal hours per calf to be confident that we accurately estimated their number of associates. For mothers, there was an even stronger relationship between number of associates and observation time ( $r_s = 0.562$ ,  $P < 0.001$ ,  $n = 49$ ). Even when the data set was limited to mothers observed 16 or more hours, the mother's number of associates still tended to be correlated with observation time ( $r_s = 0.373$ ,  $P = 0.08$ ,  $n = 23$ ). The percent time alone was also correlated with total observation time for both mothers ( $r_s = 0.446$ ,  $P = 0.001$ ,  $n = 49$ ) and calves ( $r_s = 0.395$ ,  $P < 0.001$ ,  $n = 89$ ). But if calves were observed five or more hours ( $r_s = 0.158$ ,  $P = 0.23$ ,  $n = 59$ ) and mothers observed three or

Table 1. Spearman's rank correlation matrix. For each comparison  $n = 89$  calves.

	Number of associates	Percent time in groups	Simultaneous companions <sup>a</sup>
Number of associates	–	–	–
Percent time in groups	0.503 <sup>b</sup>	–	–
Simultaneous companions	0.571 <sup>b</sup>	0.857 <sup>b</sup>	–

<sup>a</sup>“Simultaneous Companions” represents the number of associates, in addition to the mother/calf, in the group at one time.

<sup>b</sup> $P < 0.001$ .

more hours ( $r_s = 0.262$ ,  $P = 0.10$ ,  $n = 40$ ), these correlations were nonsignificant. In contrast, the percent time in groups did not correlate with the observation time for either mothers ( $r_s = 0.093$ ,  $P = 0.52$ ,  $n = 49$ ) or calves ( $r_s = 0.034$ ,  $P = 0.76$ ,  $n = 89$ ). Calves' mean number of simultaneous companions also did not correlate with hours of observation ( $r_s = 0.152$ ,  $P = 0.16$ ,  $n = 89$ ). And finally, although the measures we have presented look at different aspects of sociality, they were highly correlated with one another (Table 1).

#### Sampling Method

The assessment of calf sociality differed depending upon the method of data collection, even though the definition of association was virtually identical. In the focal data, the 10 most solitary calves spent between 30.2% and 71.3% alone ( $\bar{x} = 46.2\% \pm 4.4\%$ ), but in the survey data these same calves spent between 0% and 12.5% alone ( $\bar{x} = 3.4\% \pm 1.5\%$ ;  $34.8 \pm 11.3$  surveys per calf) (Fig. 1). Furthermore, focal and survey data were not correlated with one another ( $r_s = -0.096$ ,  $P = 0.79$ ,  $n = 10$ ) for these 10 calves.

When the comparison between survey and focal data was repeated using all 45 calves in the data set, these calves spent from 0% to 71.3% alone ( $\bar{x} = 15.0\% \pm 1.9\%$ ) in the focal data, but only from 0% to 12.5% alone ( $\bar{x} = 1.2\% \pm 0.4\%$ ; Fig. 2) in the survey data. The proportion of time calves spent in groups also differed between focal ( $\bar{x} = 48.3\% \pm 3.8\%$ ; range = 2.1%–97.5%) and survey data ( $\bar{x} = 65.5\% \pm 3.2\%$ ; range = 3.2%–100%; Fig. 3). In contrast to the results obtained using only 10 calves, focal and survey data were correlated with one another for both percent time alone ( $r_s = 0.396$ ,  $P = 0.007$ ,  $n = 45$ ) and percent time in groups ( $r_s = 0.660$ ,  $P < 0.001$ ,  $n = 45$ ) in this larger data set. However, 97.8% of calves spent some time alone in focal data, whereas only 20.0% of calves were ever sighted alone in survey data (McNemar's Chi-square:  $\chi^2_1 = 35.0$ ,  $P < 0.005$ ).

#### DISCUSSION

These results demonstrate that for each of the four different, but correlated, sociality measures we presented, individual variation was large for both mothers and dependent calves (see Gibson and Mann 2008a, b). Although the associate count for mothers was cumulative across periods with different calves, it is important to point out that this is still an underestimate of a mother's total number of associates since our data were limited to periods when a mother had a dependent calf. We

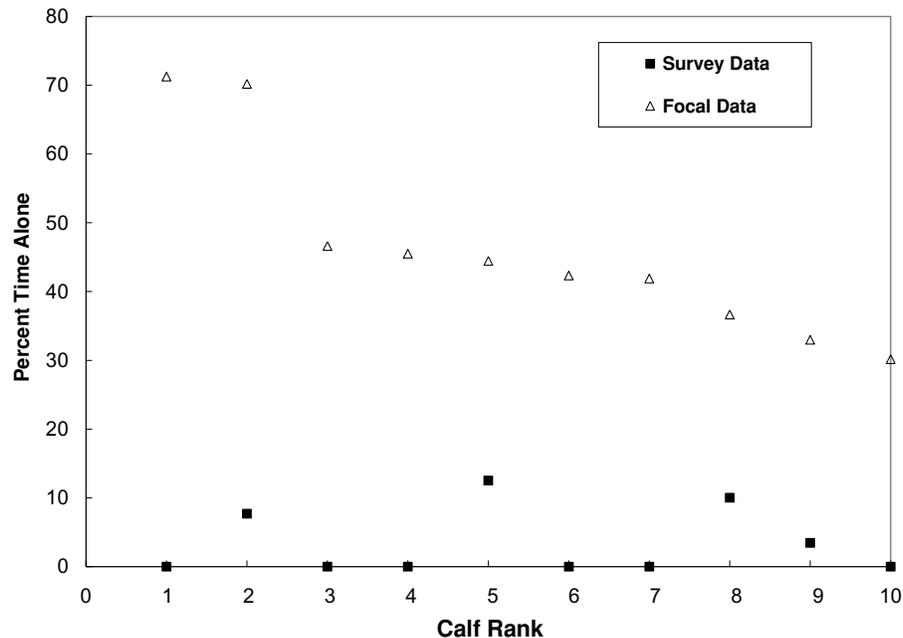


Figure 1. Comparison of 10 calves' percent time alone calculated using focal data and survey data. The 10 most solitary calves in our focal data were ranked in terms of their percent time alone. (Please note this data set was not restricted to calves observed in 10 or more surveys.) The percent time alone for these same 10 calves was then recalculated using survey data (143 surveys) instead of focal data. These measures are not correlated (Spearman's rank correlation,  $r_s = -0.096$ ,  $P = 0.79$ ,  $n = 10$ ).

also found that the amount of observation time necessary to adequately capture this variation differed depending on the measure used. The number of associates and the percent time alone were the only measures correlated with focal hours of observation. Substantial amounts of focal observation time per mother (> 16 h) or calf (> 10 h) were required to overcome the correlation between the number of associates and observation time. This is likely true for survey data as well. Fewer hours of focal observation were necessary to overcome the correlation between percent time alone and observation time for mothers (> 3 h) than calves (> 5 h), possibly because observers might wait to initiate focal sampling until the mother was sighted and calf identity was assured. And finally, we showed that measures of sociality differ depending on whether survey data or focal follow data are used. The proportion of time a calf spent in groups was almost always higher in survey data than focal follow data (Fig. 3), whereas the reverse was true for the percent time that calves spent alone (Fig. 2). Survey data may indicate relative sociality among calves because our results indicate that focal and survey data are correlated when a large enough sample size is used. However, survey data did not provide a good measure of the true values for the social measures examined. For example, the relationship between percent time alone in focal data and survey data appears to be driven by only 9 out of the 45 calves because all other calves were never observed alone in survey data (Fig. 2).

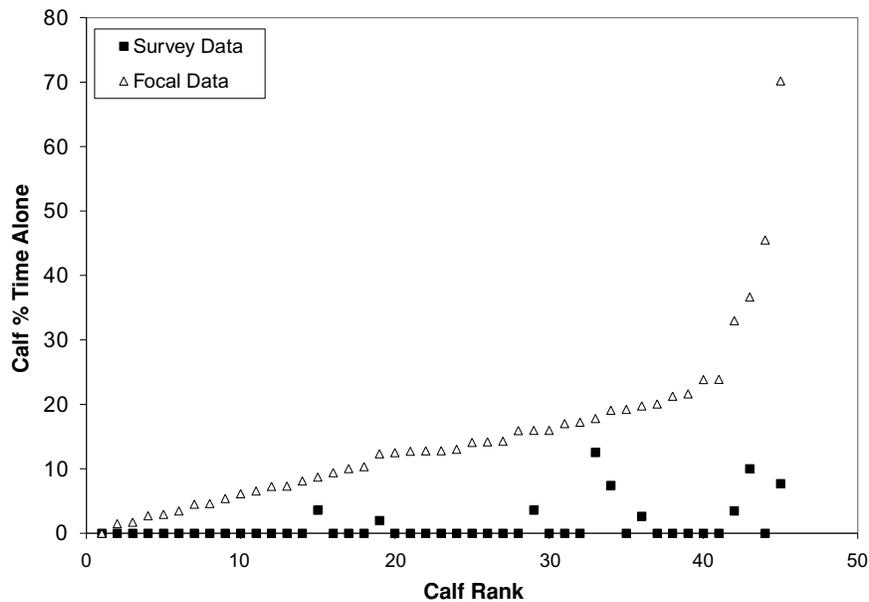


Figure 2. Comparison of 45 calves' percent time alone calculated using focal data and survey data. Calves observed in 10 or more surveys were ranked in terms of their percent time alone in the focal data. The percent time alone for these same calves was then recalculated using survey data (1,296 surveys) instead of focal data. These measures are correlated (Spearman rank correlation,  $r_s = 0.396$ ,  $P = 0.007$ ,  $n = 45$ ).

Furthermore, our first comparison using only the 10 most solitary calves indicates that survey data may provide a poor reflection of calf social patterns at the extremes. One possible reason for the discrepancy between focal data and survey data is the observer bias in survey data; lone calves are less likely to be noticed than groups of animals, so percent time alone for calves is likely to be greatly underestimated. Alternatively, the approach of an observation vessel during data collection for brief surveys may prompt calves to rejoin their mothers or other dolphins in the vicinity, whereas during periods of extensive focal observation a calf may become tolerant of the presence of the vessel. Bejder *et al.* (2006) found increased cohesion of dolphin groups in Shark Bay when vessels approached. Furthermore, although the definition for group membership (*i.e.*, the 10-m chain rule) was the same in our focal and survey data, the sampling methods were not. The difference between continuous or point sampling (focal data) *vs.* one-zero sampling within a 5-min interval (survey data) may explain the difference in our results. One-zero sampling, in which an observer records the presence or absence of a behavior during an interval (see Mann 1999), is likely to inflate scores for the presence of behaviors (*e.g.*, the proportion of surveys that calves were in groups). For example, if a calf joined its mother and/or other dolphins at any point during the first 5 min of a survey, the calf was considered to have been in a group for that survey, even though it may have been alone for the majority of the survey. However, we randomly selected 150 separations from a focal data set of 115 calves (all ages) and the duration of separations averaged  $6.91 \pm 0.54$  minutes (Mann and Gibson, unpublished data), longer than the 5-min interval

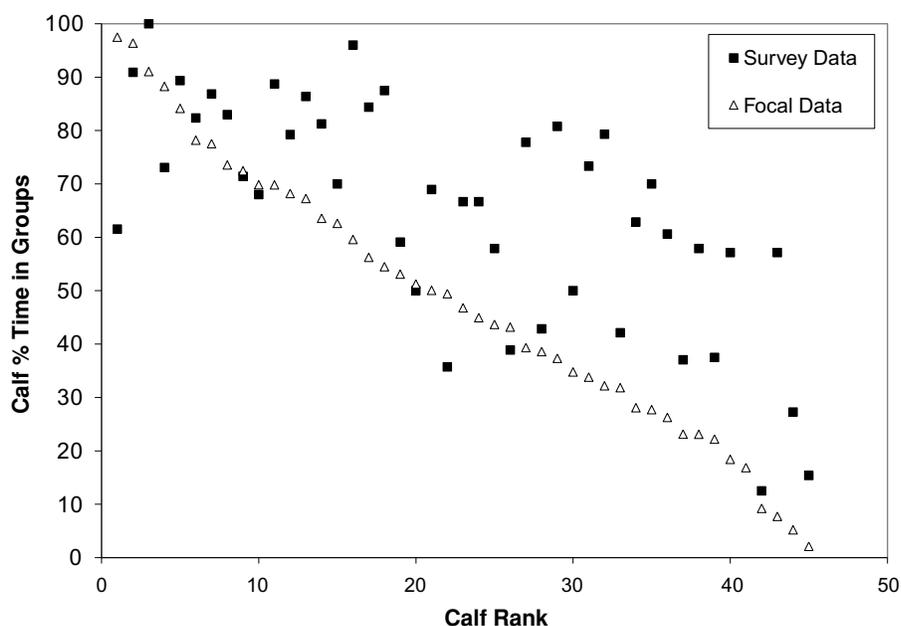


Figure 3. Comparison of 45 calves' percent time in groups calculated using focal data and survey data. Calves observed in 10 or more surveys were ranked in terms of their percent time in groups in the focal data. The percent time in groups for these same calves was then recalculated using survey data (1,296 surveys) instead of focal data. These measures are correlated (Spearman's rank correlation,  $r_s = 0.660$ ,  $P < 0.001$ ,  $n = 45$ ).

used in survey data collection. Thus, it is unlikely that the use of one-zero sampling (within a 5-min interval) instead of point sampling fully explains the conflicting results obtained from our survey and focal data. Therefore, the important message here is that the method of data collection and the amount of data do have an impact on the validity of social measures even in a well-studied population with extensive data sets. This is especially true for species with fission–fusion social organizations and high individual variation.

Mothers and calves spend substantial periods of time alone, but survey data provide a poor reflection of this. It is likely that calves at other study sites engage in frequent solitary separations as well, but this pattern is unlikely to be detected if only survey data are used. Variation in sociality is not fully captured by survey data. The inability of survey data to accurately reflect mother–calf association patterns has numerous implications. For example, if the degree of mother–calf association is used to determine weaning ages, survey data alone may not accurately depict this transition. Furthermore, calves are often overlooked or ignored in the analyses of association patterns. However, an understanding of mother–calf separations and the independent association patterns of calves are important for assessing maternal care strategies and the overall structure of a fission–fusion population. For example, strong sex differences in calf association patterns emerge preweaning and reflect underlying reproductive interests of males and females (Gibson and Mann 2008a, b). Similarly, variation in maternal socioecological strategies likely impact calf survival

and female reproductive success (Gibson and Mann 2008*a, b*). Our results suggest that an accurate representation of mother–calf social patterns can best be achieved using focal observations combined with surveys of the larger population. There is a trade-off between the sample size and the level of detail that can be obtained in the data using these two methods. While focal observations can be used to obtain highly detailed information on relatively few individuals each field season, surveys can quickly provide important information (*e.g.*, demographic) for a much larger subset of the population. Thus, a combination of adequate survey and focal sample data is ideal for assessing social patterns in species with a fission–fusion social organization.

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