

# Use of photo-identification data to quantify mother–calf association patterns in bottlenose dolphins

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**Abstract:** For social mammals living in fission–fusion societies, the mother–infant bond is long and extends beyond the nursing period. We successfully developed a technique, using photo-identification data, to quantify mother–calf association patterns in a small population of bottlenose dolphins, *Tursiops truncatus*, off eastern Scotland. By statistically comparing association indices between young calves and their associates we assigned 17 individual adults as mothers to 20 young calves with a 5% level of probability. The mean index of association between calves and mothers remained high until at least year 8 of life. While calves were still found in the same schools as their mother, they surfaced beside her less often as their age increased. This is the first time that the mother–calf bond has been quantitatively assessed for any bottlenose dolphin population inhabiting temperate waters. Results are compared with those from subtropical populations and are discussed with respect to the viability of this population.

**Résumé :** Chez les mammifères sociaux qui vivent dans des sociétés à scission–fusion, le lien mère–petit dure longtemps et se maintient au-delà du sevrage. Nous avons mis au point une technique, à base de données de photo-identification, pour quantifier les patterns d’association entre les mères et les petits dans une petite population de dauphins à gros nez, *Tursiops truncatus*, de l’est de l’Écosse. Une comparaison statistique des indices d’association entre les petits de bas âge et leurs associés a permis d’identifier 17 adultes comme des mères de 20 petits à un niveau de probabilité de 5 %. L’indice moyen d’association entre les petits et leur mère reste élevé jusqu’à au moins l’année 8 de leur vie. Bien que les petits continuent à faire partie des mêmes bandes que leur mère, ils remontent à la surface à ses côtés moins souvent à mesure qu’ils vieillissent. C’est la première fois que l’on réussit à quantifier le lien mère–petit chez une population de dauphins à gros nez dans des eaux tempérées. Nos résultats sont comparés à d’autres provenant de populations subtropicales. La viabilité de cette population fait l’objet d’une discussion.

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## Introduction

For many social mammals the mother–infant relationship is prolonged. Although infants are energetically dependent on their mothers in the first few months of life, it is thought that this protracted dependency period, often of several years, has other functions such as enhancement of survival, acquisition of cultural knowledge, and social development. Social development is particularly important for those species (e.g., African elephants, *Loxodonta africana*, chimpanzees, *Pan troglodytes*, spider monkeys, *Ateles geoffroyi*, and bottlenose dolphins, *Tursiops truncatus*) that live in fission–fusion societies, a constantly changing form of social organization in which large groups undergo fission into smaller

units and small units fuse into larger units (Lee 1986; Symington 1990; Mann and Smuts 1999).

Bottlenose dolphins are widespread and occupy a variety of climatic regions and habitats. In the subtropics calves typically remain with their mothers for 3–6 years (Shane et al. 1986; Scott et al. 1990; Wells 1991); no comparable data are currently available from temperate-zone populations. This prolonged dependency period extends beyond the 18-month nursing period observed in both wild and captive dolphins (McBride and Kritzler 1951; Tavalga and Essapian 1957; Harrison and Ridgway 1971; Perrin and Reilly 1984; Evans 1987; Cockcroft and Ross 1990a, 1990b). The proportion of time calves spend in close proximity to their mother decreases as infant age increases over the first few weeks or

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months of life (Gubbins et al. 1999; Mann and Smuts 1999). Similarly, the distance between elephant calves and their mother increases with age (Lee 1986). Female bottlenose dolphins have a minimum interbirth interval of 2 or 3 years, although 3- to 6-year intervals are more common (Connor and Smolker 1990; Scott et al. 1996; Connor et al. 2000; Mann et al. 2000). This long period of association between a calf and its mother may mean that the female will not come into oestrus until after her calf has become independent. Alternatively, as with African elephants (Lee 1986), the calf may only separate from its mother when her next calf is born.

The resident population of bottlenose dolphins that inhabits the waters off the east coast of Scotland (56–58°N) is small and geographically isolated (Wilson et al. 1999). A population viability analysis of this population predicts a decline in abundance of 5.7% per year assuming current conditions do not change (Sanders-Reed et al. 1999). It is possible that female reproductive biology may be contributing to this population's poor predicted long-term viability.

The aim of this study was to estimate, using photo-identification data that have been collected in a common format, two aspects of the reproduction of female bottlenose dolphins in this population: (1) the length of time that calves remain with their mother and (2) the proportion of time that calves spend in close proximity to their mother. Because bottlenose dolphins are not strongly sexually dimorphic, some individuals' markings are subtle, and some animals are only seen infrequently or in large groups, we found that assigning mothers to calves in the field was, at best, subjective for this population. Therefore, we developed a quantitative and objective method for assigning a mother to an identified calf using statistical comparison of association indices based on photographic samples collected through time. Photographic data typically form part of long-term studies, but are often underexploited. The method developed for this study could also be applied to the wide variety of other species and populations that are studied using photo-identification techniques.

## Methods

### Data collection

Data were derived from boat surveys (Wilson et al. 1997, 1999) carried out in the core part of the population's range in most months between 1990 and 1997, in sea states less than Beaufort Force 4. Surveys followed a predetermined route until a school of dolphins was encountered, whereupon the survey vessel slowly approached the school and ran parallel to its course. The number of individuals in the school and the location were noted and photo-identification pictures (Würsig and Würsig 1977) taken using an autofocus 35-mm camera equipped with a 75–300 mm zoom lens and ISO 100, 200, or 400 colour transparency film. A school was defined as "all animals within 100 m of each other engaged in similar activities" (after Wells et al. 1987). Individuals were identified from photographs using unique natural markings such as nicks and notches in the dorsal fin and tooth-rake marks, scratches, scars, and skin lesions on the dorsal fin and back (Würsig and Würsig 1977; Wilson et al. 1999).

All dolphins possessed sufficient markings that they could be identified from a high-quality picture. Young calves in their first year of life were distinguished from other age classes by their small size, pale skin, and the presence of foetal bands (vertical lines on the sides of the body). Between 1990 and 1997, 33 young calves were photo-identified. Juveniles differed from calves because foetal bands were no longer present.

### Assigning mothers to individual calves

For each calf we selected data collected between the date it was first photo-identified and the date it was last photo-identified in the following calendar year. Because most calves were born between July and September (Grellier 2000), this was a period of up to 18 months. The method involved calculating an index of association (Cairns and Schwager 1987; Ginsberg and Young 1992) between each identified calf and each of its associates present either in the same school or in the same photographic frame (see below). The association index ( $p$ ) was calculated as

$$[1] \quad p = \frac{x}{n}$$

where  $x$  is the number of times a calf was seen with another identified animal and  $n$  is the total number of times either animal was seen. The binomial standard error of  $p$  is estimated as

$$[2] \quad SE(p) = \sqrt{\frac{p(1-p)}{n}}$$

This index of association is thus a simple ratio index unweighted for any biases in data collection. The index of association of the top associate of each calf was compared with that of its next associate(s) using a one-tailed  $z$  test calculated using the formula

$$[3] \quad z = \frac{p_1 - p_2}{\sqrt{p(1-p)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where  $p_1 = \frac{x_1}{n_1}$ ,  $p_2 = \frac{x_2}{n_2}$ ,  $p = \frac{(x_1 + x_2)}{(n_1 + n_2)}$  (Bailey 1959).

Note that  $z$  is not a good approximation when  $n_1 + n_2 \leq 12$  (S.T. Buckland, personal communication). Associates of the calf were discounted as potential mothers if they were otherwise known to be male or had been classed as juvenile or younger in the previous year.

The method was applied in two ways using different sampling units: school and photographic frame. When encountered, schools of dolphins were classified as (i) schools in which all individuals present were photographically identified (whole schools) or (ii) schools in which not all individuals present were identified (partial schools). For partial schools there is uncertainty about whether a particular individual was present in the school and not photographed, or was not present. A photographic frame is an image of a dolphin, taken for identification purposes, that often includes the dorsal fins of other dolphins surfacing nearby at the same moment.

**Table 1.** Numbers of calves that had mothers assigned using the different methods.

	School associations (whole school identified)	School associations (all data)	Photographic-frame associations	Overall (when $n_1 + n_2 > 12$ )
Number of calves that had mothers assigned at the 5% probability level ( $n_1 + n_2 > 12$ )	8	13	7	20
Number of calves that had mothers assigned at the 5% or 10% probability level ( $n_1 + n_2$ could be $\leq 12$ in the first three columns)	14	16	8	21
Total number of calves tested	25	33	20	33

Analyses were carried out for each calf using both whole schools and partial schools. If the top associate of a calf had a significantly greater index of association than the next associate(s), this dolphin was designated the calf's mother. If there was no significant difference, the process was repeated using photographic frames in which the calf was present as the sampling unit. Using photographic frames allowed us to draw multiple samples from a single encounter with a school. As a test, the method using photographic frames was applied to one calf that had been assigned a mother by means of the schools method.

#### Length of time a calf remains with its mother

An index of association was calculated for each calf and its assigned mother for each year of the calf's life from the date it was first seen until the date it was last seen in each year. Data were then combined for the 11 calves that had been seen in 3 or more years, and a mean index of association was calculated for each year of life.

The time series of data available for each calf varied for a number of reasons. Four of the 11 calves were born near the end of the study period, thereby reducing the length of time they were available to be seen. Other possible reasons for the variable time series of data include loss of the calf from the population as a result of death or emigration; loss of marks; and the possibility that the calf was alive but not photographed in a given year. Two of these (mark loss and emigration) may cause potential bias in the results of these analyses.

Mark loss is a potential problem with calves in this population because they generally possess only temporary marks such as skin lesions and scratches. To explore whether mark loss may have truncated the time series of data for any calf, association indices were calculated for each assigned mother and her associates in the years after her calf disappeared. If mark loss was the cause of the calf's disappearance, it would be expected that a newly identified individual, of similar size to the calf, would consistently be one of the top associates of the mother. If, however, the calf had been lost from the population, or had separated from her, the mother would be unlikely to have a top associate of the correct size to be the original calf.

To explore whether the cause of the calf's disappearance was loss from the population due to death, efforts were made to match photographs of any dead stranded dolphins to those in the photo-identification catalogue.

#### Proportion of time mother and calf spent in close proximity

This was estimated using presence in individual photographic frames as a proxy for proximity of calves to other animals. Each dorsal fin in each frame was either assigned an identification number or classed as unidentifiable. For every frame in which each calf was present, the presence of the calf's mother in the frame was noted. The proportion of frames of each calf in which its mother also appeared was calculated for each year of that calf's life. Data for the 11 calves were combined, and the mean proportion of frames with the mother was calculated for each year of life.

## Results

#### Assigning mothers to individual calves

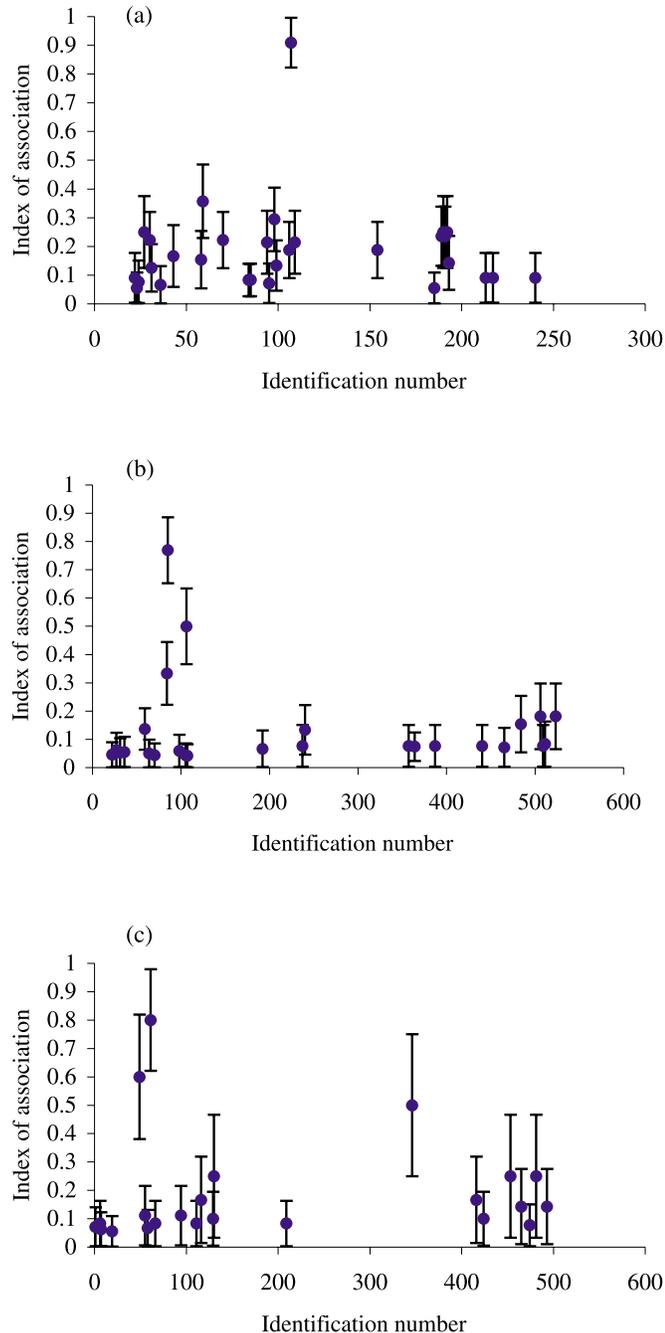
Ten of the 33 calves were identified on only a single day. The remaining calves were seen over time spans ranging from 3 to 608 days. Twenty-five of the 33 calves had been identified in at least one encounter where the whole school had been photo-identified.

Using data only from whole schools, the top associate of 12 calves had a significantly greater association index than the next top associate(s) at the 5% probability level (although in four cases samples were too small for  $z$  tests to be reliable). The top associate of two additional calves had a significantly greater association index than the next top associate(s) at the 10% probability level (Table 1). Figure 1 shows three typical association-index distributions that produced results significant at probability levels of 5%, 10%, and not significant.

Using data from all schools (whole and partial), the top associate of 14 calves had a significantly greater association index than the next top associate(s) at the 5% probability level (although in one case samples were too small for  $z$  tests to be reliable). The top associate of two additional calves had a significantly greater association index than the next top associate(s) at the 10% probability level (Table 1).

The potential for using photographic frame as the sampling unit was tested on a randomly selected calf that had been identified in seven schools and 48 frames. The top associate of the calf using both encounter and photographic frame as the sampling unit was the same individual, and it had a significantly greater index of association with the calf than the next closest associate at the 5% probability level using both methods.

**Fig. 1.** Examples of distributions of association indices ( $\pm$  standard error) that produced a significant result at the 5% probability level ( $z = 2.796$ ,  $n_1 + n_2 = 25$ ) (a), produced a significant result at the 10% probability level ( $z = 1.447$ ,  $n_1 + n_2 = 27$ ) (b), and did not produce a significant result ( $z = 0.690$ ,  $n_1 + n_2 = 10$ ) (c).



Photographic frame was used as the sampling unit for the 20 remaining calves that had not been assigned a mother at the 5% probability level when school was used as the sampling unit. These calves had been identified in between 1 and 85 photographic frames. The top associate of seven calves had a significantly greater association index than the next top associate(s) at the 5% probability level, and one

other animal had a significantly greater association index than the next top associate(s) at the 10% probability level (Table 1). A further six calves had only one associate that occurred in the same frame, which suggests that this individual could be its mother. However, with no other associate to test against, the method cannot be used in these cases.

In summary, 17 different individuals were quantitatively assigned as mothers of calves. Two mothers were assigned to multiple calves during the study period. These births occurred at 2-year intervals and in both cases the previous calf died, or disappeared, prior to the birth of the next calf.

#### Length of time a calf remains with its mother

The length of time that calves remained with their mother varied from 3 to at least 8 years. The level of association between calves and their mothers also varied. Some calves remained highly associated with their mother, while the association indices of others were more variable from year to year.

The mean index of association between mother and calf was 0.9 or greater for the first 3 years of life. For years 4–8 of life it decreased to approximately 0.7 (Fig. 2), suggesting a step down from a period of constant high association to a period of constant lower association.

The top associates of six mothers whose calves disappeared were examined to investigate the possibility that the disappearance of their calves could have resulted from mark loss. The age classes of their subsequent top associates were adult, subadult, or calf in its first year of life. Because none of the missing calves could have become adult or subadult in the period after their disappearance, and they were all more than 1 year old when they disappeared, these results should not be biased because of mark loss.

No matches were made between recovered dead dolphins and photo-identified animals.

#### Proportion of time mother and calf spent in close proximity

The proportion of time calves spent in close proximity to their mother decreased in an apparently linear fashion over the first 7 years of life, from 0.55 in year 1 to 0.1 in year 7 ( $r^2 = 0.888$ ,  $p < 0.001$ ,  $y = -0.073x + 0.645$ ; Fig. 3).

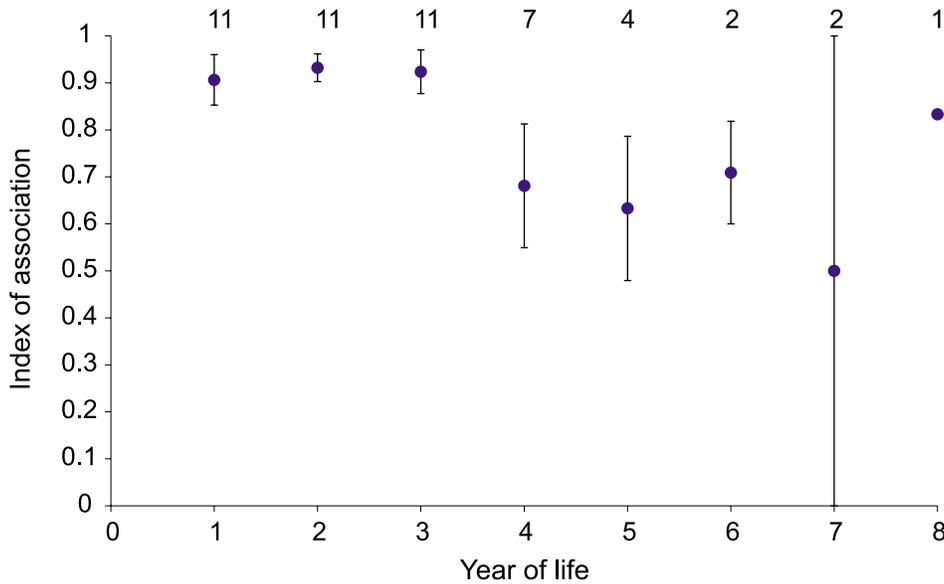
## Discussion

#### Assigning mothers to individual calves

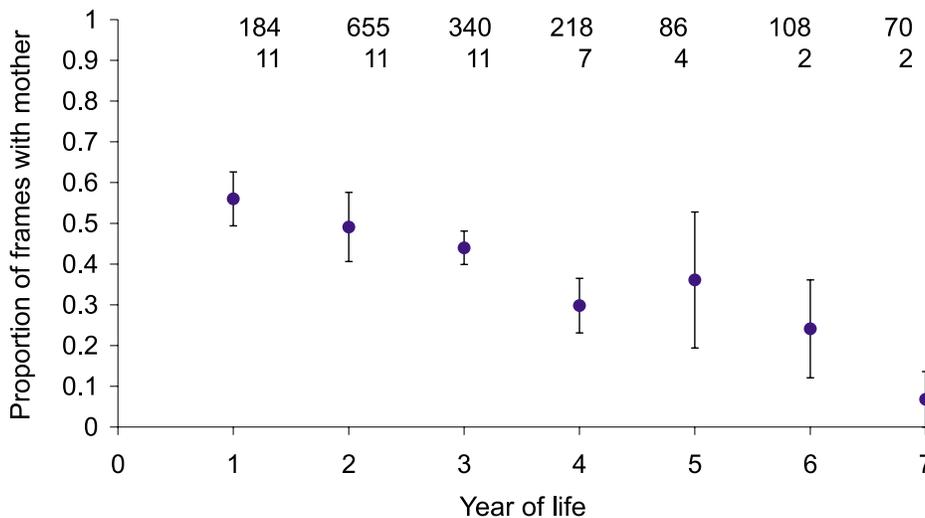
Using a statistical comparison of association indices to identify the closest associate of young calves provides an objective and quantifiable method for assigning the individual most likely to be its mother. The method also allows this individual to be assigned with a level of probability. By using encounters with whole school, then partial school, and finally photographic frame as the sampling unit we have a hierarchical method of extracting information from photo-identification data.

Without additional information, we can only assume that the top associate is the mother of the calf. This assumption could be tested using data from a study in which photo-identification data have been collected alongside tissue sampling and subsequent maternity analysis.

**Fig. 2.** Indices of association (mean  $\pm$  standard error) between calves and their mothers in each year of life. The number above each data point is the number of calves.



**Fig. 3.** Proportions of time (mean  $\pm$  standard error) calves spend with their mothers in each year of life. The upper row of numbers above each data point shows the number of photographic frames and the lower row shows the number of calves.



**Length of time a calf remains with its mother**

The mean index of association between calves and their mothers remained high until at least year 8 of life. This contrasts with bottlenose dolphin mothers and their offspring in the Indian Ocean, who associated consistently only throughout the calf’s first 4 years of life (Smolker et al. 1992). The results from our study are more similar to those from Sarasota, Florida, where calves have been known to remain with their mothers for up to 10 years (Wells et al. 1987; Wells 1991). Data in this study were collected from just 1990 to 1997, and with a longer time series of data we may find that the mean index of association remains high for even longer than the 8 years we report here.

There are several possible functions, and implications, of this seemingly long period before mother–calf separation. One explanation is that interbirth intervals are long and

calves naturally stay with their mother until her next calf is born. However, there is much inter- and intra-population variation in the timing of separation. There are documented cases in which separation occurred while the mother was pregnant, soon after the birth of the mother’s next calf, apparently years before the next birth, and also cases in which the calf stayed with its mother after her next calf was born (Wells et al. 1987; Wells 1991; Mann and Smuts 1999; Connor et al. 2000; Mann et al. 2000).

Notwithstanding this variability, the long period before separation of calves from their mothers suggests that the interbirth interval for this population may be long. Even if female longevity in this population is similar to that observed in others (Scott et al. 1996), this would mean that females could produce few calves in their lifetime. This could severely affect the viability of the population.

The disappearance of some calves from the population after only 3 or 4 years of life was likely a result of death or emigration. That no suitable candidates for the calves were found among their mothers' associates after their disappearance suggests that separation was not an artifact of mark loss. However, it is possible that these calves were photographically sampled after separation but were not recognized, owing to mark loss. If this was the case, the data would be biased by the tendency to include animals that stayed with their mother but to exclude those that did not. Note that no bias results if calves were simply not photographed by chance or if they died. No matches were made between dead stranded dolphins and those in the photo-identification catalogue, but the condition of stranded animals makes many unrecognizable and not all animals that die will wash ashore. If calves that disappeared had emigrated, a bias similar to that due to mark loss would result. However, photographic surveys have also been conducted in other areas along the Scottish east coast (University of Aberdeen / Sea Mammal Research Unit, unpublished data) at what are currently believed to be the extremities of this population's range, and there is no evidence of new populations being founded in other areas. We believe, therefore, that the likelihood of bias due to emigration from this population is minimal.

#### Proportion of time mother and calf spent in close proximity

While calves up to 7 years old were often found in the same schools as their mother, they surfaced beside her less often as their age increased. If female bottlenose dolphins do not come into oestrus again until their calf is independent, the proportion of time that calves spend in close proximity to their mother will affect her reproductive status. At 1 year old, calves were spending approximately 50% of their time in close proximity to their mother. This result is comparable to those from other studies covering the first 10 weeks and 12 months of life of both wild and captive bottlenose dolphin calves (Gubbins et al. 1999 ( $n = 6$ ); Mann and Smuts 1999 ( $n = 9$ )). In this study, photo-identification data allowed us to examine this parameter over a longer time scale (7 years) and for more individuals ( $n = 11$ ). Although these data were not collected for this purpose, they have proved valuable in the study of mother-calf interactions. Intensive follows of wild dolphins (Mann and Smuts 1999; Smolker et al. 1992) and photo-identification (this study) both have advantages and disadvantages as regards cost, disturbance, and investment of time.

Given the population estimate of 129 individuals (Wilson et al. 1999), and the likely sex and age ratios, the 17 animals assigned as mothers are likely to represent a reasonable sample of the reproductive females present in this small and isolated bottlenose dolphin population on the Scottish east coast. Because these mothers are individually recognizable, we can continue to record their calving histories and begin to estimate interbirth intervals with a view to estimating population parameters such as reproductive and growth rates (Barlow and Clapham 1997). Given the vulnerability of this small population (Sanders-Reed et al. 1999; Wilson et al. 1999; Thompson et al. 2000), this would be a valuable exercise in monitoring the fate of the population in the future.

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