

Coefficients of association of reproductively active female Atlantic spotted dolphins, *Stenella frontalis*

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Abstract

From 1985-1996, a resident pod of Atlantic spotted dolphins has been extensively observed and studied off Little Bahama Bank, Bahamas. Of 157 identified individuals, 16 females of reproductive age, and 35 of their offspring, were chosen for analysis. Coefficients of association (COA) among these 35 mother/calf pairs, and the identified population, were determined using a half-weight index. Values were compared between years and through changes in reproductive status.

Mother/infant pairs showed high COA's (means ranging from 0.96 to 0.85) from birth through the first three years. COA's remained high until the year of the birth of subsequent siblings. At that time, a significant decrease in association values between the calf and the mother occurred. Juvenile females displayed strong associations (values ranging from 0.43 to 0.67) with other females in the same age class. These values dropped significantly upon sexual maturity and between years of changing reproductive condition. Pregnant females formed significant associations (values ranging from 0.10 to 0.89) with previously unassociated females who also gave birth the same year. Ten of the nineteen new associations continued at a stable level for two or more years.

Changes in reproductive state in female Atlantic spotted dolphins had a significant impact on female/female association patterns. The effects were specifically profound for first parturition females and less so for experienced females.

Introduction

Understanding the behavior, life history, and population biology of species are important in the analysis of social structure, conservation science and evolution (Slooten *et al.*, 1993). The dynamics

of associations, between individuals during developmental and reproductive stages, can shed light on aspects of the social structure of a population.

The social structure and long-term relationships of odontocetes have been reported for the bottlenose dolphin, *Tursiops truncatus*, (Wells *et al.*, 1987; Connor *et al.*, 1992; Smolker *et al.*, 1992), Hector's dolphin, *Cephalorhynchus hectori*, (Slooten *et al.*, 1993), killer whales, *Orcinus orca*, (Bigg *et al.*, 1990; Heimlich-Boran, 1993), short finned pilot whales *Globicephala macrorhynchus*, (Heimlich-Boran, 1993), and sperm whales, *Physeter macrocephalus*, (Whitehead *et al.*, 1991).

The long-term relationships of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, have not been previously investigated. A population of spotted dolphins has been studied in the Bahamas since 1985 (Byrnes *et al.*, 1989; Herzing, 1996, 1997). This paper reports on changes in coefficients of association for reproductive females in this population, over a twelve year period.

Methods

Atlantic spotted dolphins were encountered over shallow sand banks, ranging in depth from 6-16 m, off Grand Bahama Island in the Bahamas. In 1070 days at sea between May 1985 and August 1996, dolphins were encountered on 644 days. An encounter was defined as any period of time spent with the same group of identifiable dolphins. During an encounter, anywhere from one to 50 spotted dolphins were observed at the surface and from underwater. These dolphins have been habituated to human presence in the water and continue to be observed as part of an ongoing long-term study.

Individual dolphins ($n=157$) were identified using surface and underwater photo-identification techniques, documenting their dorsal fin, fluke, scars, and spot patterns. Sex was determined by direct observation of the genital area. Presence of mammary slits was used for defining females.

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Age classes were determined initially by using the ontogenetic classification system of the pan tropical spotted dolphin, *Stenella attenuata*, which correlates color and spotting phase with maturity (Perrin, 1970). Age classes were updated by tracking their actual spot development over the years (Herzog, 1997).

Sixteen reproductively active females, and 35 of their offspring were included in this analysis. Reproductive state was determined for females by visual inspection. Females were classified as reproductively active when they were observed (1) visibly pregnant (approximately six months into gestation), (2) lactating, with distended mammarys, or (3) nursing a calf. Females were considered of reproductive age if they were mottled or fused, regardless of known reproductive success. The gestation period is unknown for the Atlantic spotted dolphin. Since the gestation for pantropical spotted dolphins is estimated to be 11.5 months (Perrin *et al.*, 1976) and bottlenose dolphins at one year (Schroeder 1990), we assumed a one-year gestation, with unknown variance, for Atlantic spotted dolphins.

A half-weight index was used to determine coefficients of association (COA) for each of the study dolphins (Cairns & Schwager 1987).

$$\text{Half Weight Index} = \frac{x}{x+1/2(Ya+Yb)}$$

where x is the number of encounters that included both dolphins a and b , Ya is the number of encounters that included dolphin a but not dolphin b , and Yb is the number of encounters that included dolphin b but not dolphin a . These association indices range from 0.00 for two dolphins that are never seen together, to 1.00 for two dolphins that are always seen together. Differences between association values were tested for significance ($P < 0.05$), using the Kruskal-Wallis ANOVA tests.

Female spotted dolphins that produced successful offspring (i.e. offspring that survived for at least one year) were selected for consideration in determining associations between mothers and calves. Of these females, only individuals that were seen consistently during the study period were examined. The COA values of the mothers and their calves were determined and tracked from birth year to year 11 (the longest complete association on record in the study area). Relative birth years were listed as year 1, yearlings were year 2, up to the eleventh year.

Coefficient values were determined for mother/calf pairs for the years before, during and after the birth of a subsequent calf. Again, values were relative and birth years were aligned.

Associations between females at first parturition were calculated for three female dolphins who became mature during the study period. Association values of three females, with each other and with all available reproductively aged females, were tracked and compared from year to year.

Associations between new mothers and experienced females with same birth years were determined using values for 'first time' mothers and experienced females that gave birth in the same year. These COA values were tracked, compared and tested for significant changes between the seasons before, during and after the new mother's first pregnancy. Relative birth years, regardless of the actual date, were ranked and compared.

Experienced and first parturition females were combined to examine association values between twelve reproductively successful females and thirteen reproductively aged females. These COA values were tracked and tested for significant changes between the two years before and two years after parturition. Birth years were aligned regardless of absolute year. Some individual females were considered in this study more than once, if they had more than one successful pregnancy during the study period. Coefficients of association values were tracked and tested for significant changes between years.

Results

Associations between mothers and calves

The highest COA values tracked in this study were between mother and calf pairs during the first three years, with mean values ranging from 0.96-0.85 (Fig. 1). During the first year, the mean COA value was 0.96. There was a significant drop in association values between the birth year and the second year ($P = 0.0035$). Between the third and fourth year another significant change in association occurred ($P = 0.0041$) when mean COA values dropped to 0.58. Although sample sizes were low for years eight through eleven ($n \leq 4$), there continued to be consistent association values between mothers and calves.

Thirteen calves, whose mothers did not give birth in the average interval of three years, retained higher COA values with their mothers in years four and five than offspring who had a sibling born those years. Significant drops in these values ($P = 0.0001$) corresponded with the subsequent pregnancy of the mother or the birth of a calf that was lost (Table 1).

Associations between females at first parturition

During this study, three dolphins matured into reproductively active females. Little Gash (LG), Mugsy (MU), and Rosemole (RM) were highly associated during their early years as juveniles from

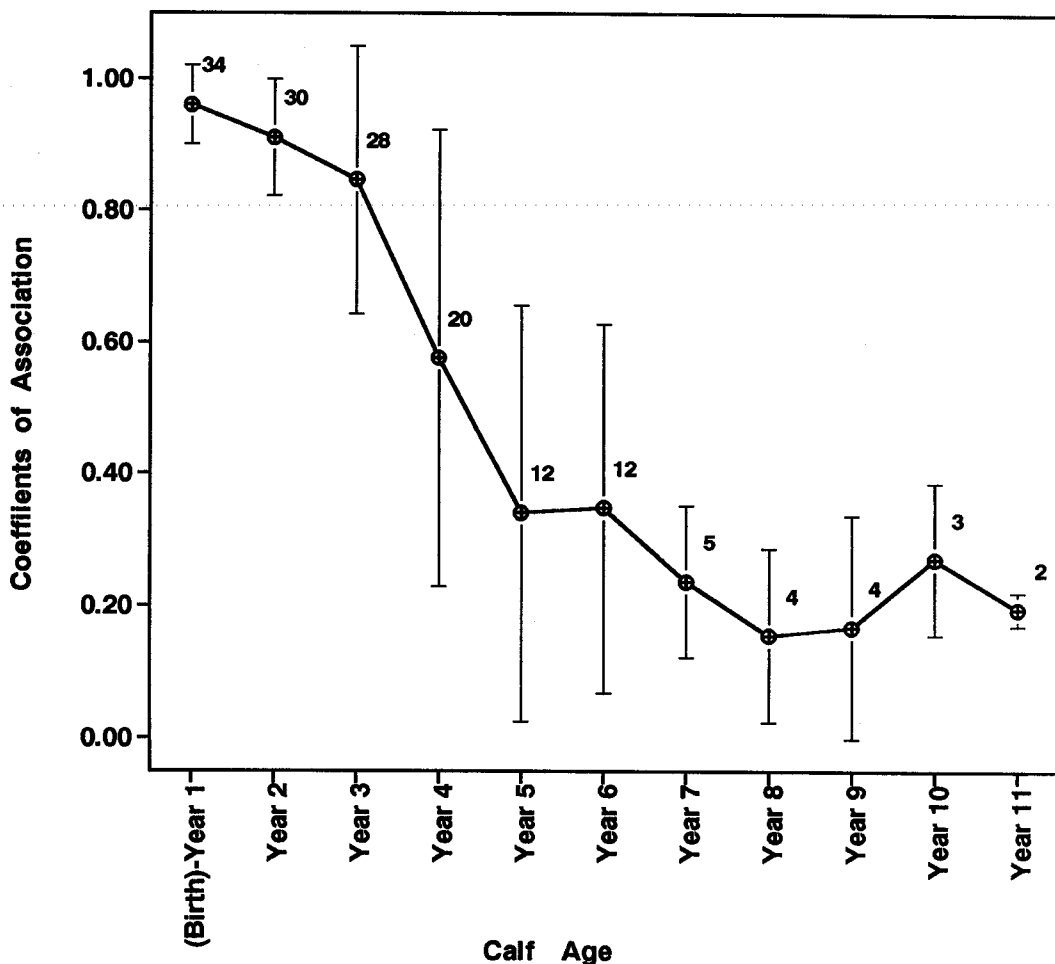


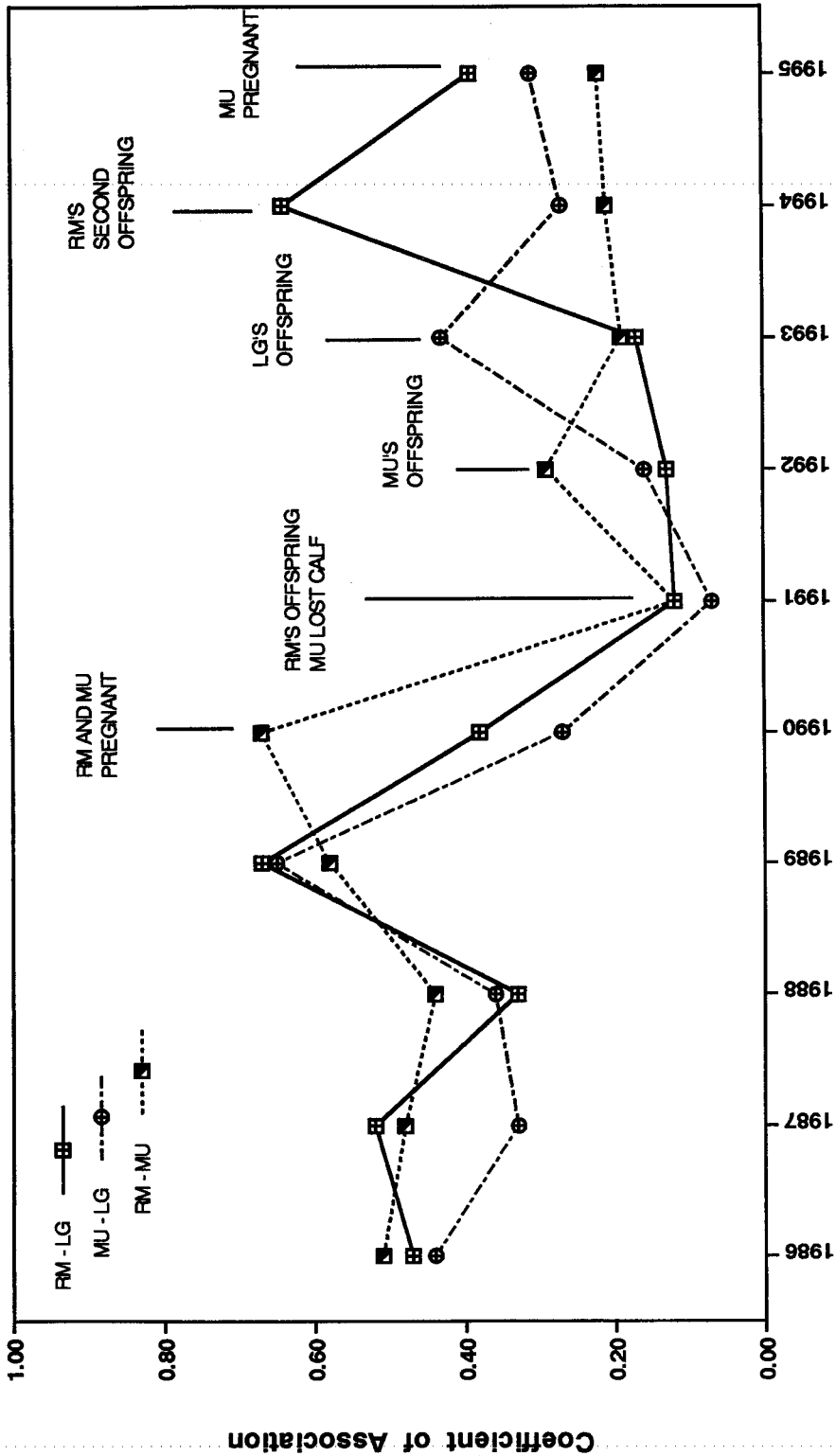
Figure 1. Coefficients of association between mothers and their calves over time. The mean, standard deviation, and n are given.

Table 1. Range of coefficient of association values for thirteen offspring whose mothers did not give birth in a three year interval. MRS is the Mother's Reproductive Status the last year (and lowest value) with offspring

| Females | Range | Years | MRS | Males | Range | Years | MRS |
|---------|-----------|-------|------|-------|-----------|-------|-------|
| Gemer | 0.75-1.00 | 4 | — | Geo | 0.89-1.00 | 5 | — |
| LHali | 0.96-1.00 | 4 | — | Hav | 0.86-0.96 | 4 | — |
| Sym | 0.67-0.92 | 4 | — | Leo | 0.25-0.91 | 4 | Birth |
| Pict | 0.67-1.00 | 4 | Preg | Lat | 0.84-0.94 | 4 | — |
| Brush | 0.80-1.00 | 4 | — | Mel | 0.36-0.97 | 4 | Preg |
| Snow | 0.92-1.00 | 4 | — | Prov | 0.86-1.00 | 4 | — |
| | | | | Poin | 0.67-1.00 | 5 | Birth |

1986-1989 (Fig. 2). These strong associations continued until RM and MU became pregnant in 1990, at which time both MU's and RM's COA values

with LG dropped while their values with each other increased. MU lost her calf and was pregnant again in 1991, when RM's COAs with both MU and



YEAR

Figure 2. Changes in coefficients of association between three maturing females, Rosemole (RM), Little Gash (LG), and Mugy (MU) from 1986-1995. Pre-parturition, parturition, and post-parturition activity is presented.

LG dropped from 0.67 to 0.12 and 0.38 to 0.12 respectively.

Each first parturition female showed increased association with members of the triad who had given birth the previous year. In 1992, MU gave birth and her COA with RM, a mother from the previous year, increased from 0.12 to 0.29. In 1993 the third 'first time mother' LG gave birth and her COA with MU, a mother from the previous year, increased from 0.16 to 0.43. The following year (1994) RM gave birth to a second offspring, and her COA with LG, a mother from the previous year, increased from 0.17 to 0.64. Association values between RM and MU remained consistent between 1993 through 1995 (0.19 to 0.22) despite MU's pregnancy in 1995. Although there was an increase, the post-partum levels did not revert to the pre-maturity levels of association. COA values between RM and LG dropped (0.64 to 0.39) in 1995 while both females were nursing their young.

Associations between mothers with same birth years
Between their pregnancy year and birth year, first parturition females had significant increases ($P=0.0062$) in their association patterns with females of the same or within one-year of a similar reproductive condition (Table 2). The same females also had significant decreases ($P=0.0225$) in their association patterns, between the first and second years following parturition.

1991 birth year. RM formed higher associations (0.25–0.30) in 1991 and 1992 with three females (HE, GE, LI), who also gave birth in 1991, than for the two years prior to their same year birth (0.00–0.13).

1992 birth year. Although there were no other birth year females in 1992, MU increased her associations with three mothers with one-year-old calves (HE, LU, RM). HE was an experienced female with no previous associations with MU prior to one year before MU's first parturition. LU was an experienced female with only a low level of association with MU prior to one year before MU's parturition. RM was an inexperienced female with high association with MU during developmental years (see Fig. 2). COA values ranged from 0.08–0.55 for these females between one year prior and one year following MU's parturition year.

1993 birth year. In 1993, when LG gave birth for the first time, she established associations (0.12–0.29) with two previously unassociated females, DO and ME, who also gave birth that year. In addition, LG established an association, during her pregnancy year, with PR1, who also gave birth in 1993. Associations with DO and ME lasted through the

birth and following year, but dropped to 0.00 in 1995. DO, ME, and PR1 were all mature females who had previous offspring. Their COAs were low (0.00–0.10) with each other during 1993. Instead, they established associations only with LG, the maturing female who was giving birth for the first time.

Associations between all reproductively active females during reproductive intervals

Ten reproductive females of all ages, monitored for two years before and two years after the birth of their offspring, were tested for changes in their relationships with each other and other reproductively active females.

There was a significant change between conception and birth years and no significant changes in association values prior to the conception year or from the birth year through the post-pregnancy years (Table 3).

Associations between all reproductive aged females over a ten year period

Significant changes for all reproductively aged females, over a ten year period, regardless of reproductive activity, occurred only between 1990–1991 ($P=0.0000$) and 1994–1995 ($P=0.0366$). 1991 and 1995 were both heavy birth years (>5 calves), where twelve and seven calves were born respectively.

The three females who gave birth for the first time during this study, had significant change in association values with the reproductively aged female population only in 1990–1991 ($P=0.0283$).

Discussion

Quantifying association patterns is a useful technique for understanding spotted dolphin social organization. COA values were found to correspond to a variety of reproductive parameters. Spotted dolphin mothers and their calves had high COA's during the first three years. This is similar to findings for bottlenose dolphins in Sarasota Florida (Wells *et al.*, 1987) and in Monkey Mia, Australia (Smolker *et al.*, 1992). Recent analysis of long-term reproductive intervals in this *Stenella* population show that mothers, with calves that survive the first year, have reproductive intervals with an average of 3.56 years (Herzing, 1997). The drop in COA values between years three and four support a natural break in mother/calf relationships after the birth of a subsequent offspring. Older spotted dolphin calves, whose mothers had not yet given birth to another offspring, maintained high association values with their mothers until the mothers became pregnant again, sometimes up to five years.

Developmental aspects, as well as parturition, may contribute to the changing COA values

Table 2. Coefficient of association values for first parturition females and females with similar reproductive state

| Mother and birth year | Associate female | Two years prior to birth | One year prior to birth | Parturition | One year after birth | Two years after birth |
|-----------------------|------------------|--------------------------|-------------------------|-------------------|----------------------|-----------------------|
| RM (1991) | GE | 0.08 | 0.13 | 0.26 | 0.00 | 0.18 |
| | HE | 0.08 | 0.00 | 0.30 | 0.29 | 0.22 |
| | LI | 0.10 | 0.00 | 0.25 | 0.21 | 0.00 |
| MU (1992) | HE | 0.00 | 0.08 | 0.34 | 0.55 | 0.09 |
| | LU | 0.14 | 0.10 | 0.32 | 0.28 | 0.22 |
| | RM | 0.67 | 0.12 | 0.29 | 0.19 | 0.21 |
| LG (1993) | DO | 0.00 | 0.00 | 0.29 | 0.32 | 0.00 |
| | ME | 0.00 | 0.00 | 0.12 | 0.23 | 0.00 |
| | PR1 | 0.00 | 0.43 | 0.22 | 0.32 | 0.18 |
| P values | | Year | Year | Year | Year | Year |
| | | \leftrightarrow | \leftrightarrow | \leftrightarrow | \leftrightarrow | \leftrightarrow |
| | | $P=0.8119$ | $*P=0.0062$ | $P=0.5956$ | $*P=0.0225$ | |

*Significant at 0.5.

Table 3. Changes in associations between all reproductively aged females during reproduction intervals

| Year | Two years to one year pre-partum | One year pre-partum to parturition year | Parturition year to one year post-partum | One to two years post-partum |
|---------|----------------------------------|---|--|------------------------------|
| P value | 0.2325 | 0.0310* | 0.5238 | 0.7357 |

*Significant at 0.05.

between spotted dolphin mothers and calves. The timing of the birth of a sibling may affect the relationship of previous offspring with the mother. Such ontological stages are also important to other social mammals including primates (Goodall, 1986), and elephants (Moss & Poole, 1983).

Reproductive state, especially first parturition, had significant effects on relationships between maturing female spotted dolphins. Females developed new female associations with other females of similar reproductive state if their current associates did not share a similar reproductive condition. Bottlenose dolphins in Sarasota also show a close relationship between reproductive condition and degree of association (Wells *et al.*, 1987).

Although first parturition females formed new and strong associations with older females with the same birth year, older and experienced females did not form new or significant associations with previously unassociated females. This supports the hypothesis that it may be critical for females giving birth for the first time to be around females with experience, but mature females with multiple offspring may have solidified their long-term female relationships. Similar aspects of the importance and social function of experienced females has been described in other delphinid societies (Norris & Pryor, 1991).

Other factors may effect changes in associations between females including changing energetic needs and foraging strategies of pregnant and lactating individuals. In a study of pan tropical spotted dolphins, *Stenella attenuata*, pregnant dolphins consumed more squid (which were higher in water content) than fish and lactating dolphins consumed more flying fish (which were higher in fat), than squid (Bernard & Hohn, 1989). Young & Cockroft (1994, 1995) reported that pregnant common dolphins (*Delphinus delphis*) consume a larger proportion of fish than lactating females who prioritize the consumption of cephalopod prey. Behavioral influences of conspecifics including courtship and mating activity may also affect changes in associations. Although behavioral indicators in reproductive activity have been reported in primates (DeWaal, 1982; Goodall, 1986), they have had mixed results from delphinids regarding the ability to determine future pregnancy (Connor

et al., 1992) and the inability to predict estrous cycles (Benirschke *et al.*, 1980; Schroeder, 1990; Wells, 1984).

Careful monitoring of changes in COA values of maturing females, as well as those between females with similarly aged calves, may be useful as an indicator of changing reproductive requirements and relationships in delphinid populations.

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References

- Bernard, H. J. & Hohn, A. A. (1989) Differences in feeding habits between pregnant and lactating spotted dolphins *Stenella attenuata*. *Journal of Mammalogy* **70**(1), 211-215.
- Benirschke, K., Johnson, M. L. & Benirschke, R. J. (1980) Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation induced? *Fishery Bulletin* **78**(2), 507-528.
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. B. & Baclomb, K. C. (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm. Spec. Iss.* **12**, 383-405.
- Byrnes, P. E., Black, N. A. & Leatherwood, S. (1989) Photo-identification, behavior and distribution of spotted dolphins *Stenella frontalis* in the Bahama Banks. Abstract. In: *Proceedings of the Eighth Biennial*

- Conference on the Biology of Marine Mammals. Pacific Grove, CA. 7–11 December, 1989. p. 10.
- Cairns, S. J. & Schwager, S. J. (1987) A comparison of association indices. *Animal Behavior* **35**, 1454–1469.
- Connor, R. C., Smolker, R. A. & Richards, A. F. (1992) Two levels of alliance formation among male bottlenose dolphins *Tursiops* sp. *Proc. Natl. Acad. Sci. USA* **89**, 987–990.
- Dewaal, F. (1982) Chimpanzee Politics: Power and Sex among Apes. San Francisco: Harper and Row.
- Goodall, J. (1986) Chimpanzees of Gombe: Patterns of Behavior. Belknap Press of Harvard University Press: Cambridge, Massachusetts.
- Herzing, D. L. (1996) Vocalizations and associated underwater behaviour of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphin, *Tursiops truncatus*. *Aquatic Mammals* **22**(2), 61–79.
- Herzing, D. L. (1997) The Natural History of the Atlantic Spotted Dolphin *Stenella frontalis*: Age Classes, Spotting Patterns, and Female Reproductive Intervals. *Marine Mammal Science* **13**(4), 576–595.
- Heimlich-Boran, J. R. (1993) Social Organization of the Short-Finned Pilot Whale, *Globicephala macrorhynchus*, with Special References to the Comparative Social Ecology of Delphinids. Doctoral thesis, Cambridge University. 134 pp.
- Heimlich-Boran, S. L. (1988) Association Patterns and Social Dynamics of Killer Whales, *Orcinus orca*, in Greater Puget Sound. Thesis, San Jose State University. 98 pp.
- Moss, C. J. & Poole, J. H. (1983) Relationships and Social Structure of African Elephants. In: R. S. Hinde (ed.) *Primate Social Relationships*. pp. 315–325. Blackwell Scientific Publications: Oxford.
- Norris, K. S. & Pryor, K. (1991) Some Thoughts on Grandmothers. In: K. Pryor & K. S. Norris (eds) *Dolphin Societies*. pp. 287–289. University of California Press: Berkeley and Los Angeles.
- Perrin, W. F. (1970) Color Pattern of the Eastern Pacific Spotted Porpoise *Stenella graffmani* Lonnberg (Cetacea, Delphinidae). *Zoologica (NY)* **54**, 135–149.
- Perrin, W. F., Coe, J. M. & Zweifel, J. R. (1976) Growth and Reproduction of the Spotted Porpoise, *Stenella attenuata*, in the Offshore Eastern Tropical Pacific. *Fishery Bulletin* **74**, 229–269.
- Schroeder, J. P. (1990) Breeding Bottlenose Dolphins in Captivity. In: S. Leatherwood & R. R. Reeves (eds) *Bottlenose Dolphins*. pp. 435–446. Academic Press: San Diego.
- Slooten, E., Dawson, S. M. & Whitehead, H. (1993) Associations Among Photographically Identified Hector's Dolphins. *Can. J. Zool.* **71**(11), 2311–2318.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. (1992) Sex Differences in Patterns of Association among Indian Ocean Bottlenose Dolphins. *Behaviour* **123**(1–2), 38–69.
- Wells, R. S., Scott, M. D. & Irvine, A. B. (1987) The Social Structure of Free-ranging Bottlenose Dolphins. In H. H. Genoways (ed.) *Current Mammalogy*, Volume 1. pp. 247–305. Plenum Press: New York and London.
- Wells, R. S. (1984) Reproductive Behavior and Hormonal Correlates in Hawaiian Spinner Dolphins, *Stenella longirostris*. *Rep. Int. Whal. Commn. (Special Issue 6)*: pp. 465–472.
- Whitehead, H., Waters, S. & Lyrholm, R. (1991) Social Organization of Female Sperm Whales and Their Offspring: Constant Companions and Casual Acquaintances. *Behav. Ecol. Sociobiol.* **29**, 385–389.
- Young, D. D. & Cockcroft, V. G. (1994) Diet of Common Dolphins (*Delphinus delphis*) off the South-East Coast of Southern Africa: opportunism or specialization? *Journal of Zoology (London)*, **234**, 31–53.
- Young, D. D. & Cockcroft, V. G. (1995) Stomach Contents of Stranded Common Dolphins *Delphinus delphis* from the South-East of Southern Africa. *Zeitschrift für Säugetierkunde* **60**, 343–351.