

INDIVIDUAL DIFFERENCES IN BOTTLENOSE DOLPHIN INFANTS

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This paper explores some of the characteristics that are shared by dolphins and primates and distinguish them, with particular emphasis on the development of individual differences. Some preliminary data on the development of wild bottlenose dolphins are presented. These data illustrate the stability of mother-infant contact over time, a striking contrast to the patterns found in most mammals, and the individual variability of exploratory behavior (time away from mother). The latter is consistent with the inhibited-disinhibited, bold-shy, or restrictive vs. laissez-faire differences found in many species of primates, including humans. These patterns are discussed in relation to the dolphin's social ecology and life history.

INTRODUCTION

Although dolphins (family *Delphinidae*) have long attracted both popular and scientific interest, there are few systematic studies of wild dolphin behavior (Mann, in press). But captive and long-term studies on several species, particularly bottlenose dolphins, *Tursiops truncatus*, have begun to unravel some of the mysteries of their intricate lives. On the one hand, dolphins have evolved many unique features among mammals, yet on the other hand, they have converged with primates and other socially complex mammals. This paper will discuss some of the dolphin's unique and convergent features with a focus on the development of individual differences among one relatively well studied species, the bottlenose dolphin. The relations between these features and the development of individual differences in bottlenose dolphins provides a window into the adaptive problems they face and the strategies they have evolved to solve them.

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PRIMATES AND DOLPHINS: SIMILARITIES AND DIFFERENCES

Cetaceans and primates, unlike the majority of mammalian species, produce precocial young (Derrickson 1992). Characteristic of precocial species, neonates are heavier and born after longer gestation periods than altricial species (Martin and MacLarnon 1985). For cetaceans, the selective pressures favoring precocial development are obvious. They must swim and breathe independently from birth. Neonates must stay with and nurse from a constantly moving mother. Among some mammalian taxa, lactation period and precociousness are negatively correlated (Derrickson 1992). That is, large, precocious offspring are nursed for shorter periods than smaller altricial offspring. However, in primates and delphinids, the opposite seems to be true. Primate and delphinid mothers produce heavy, well developed offspring and continue to nurse them for longer than expected for a given body size. This pattern is even more pronounced in bottlenose dolphins, whose large, well-developed and motorically independent offspring are nursed for three to six years, and begin to reproduce in their early teens (Wells et al. 1987).

Paradoxically, bottlenose dolphins have rapid motor development but delayed social maturation. In developmental terms, their precocious locomotion and following response to the mother is similar to the follower strategy found among many ungulate species (e.g., Ralls et al. 1987). Yet, the delphinid's hunting ecology may be compared to that of a terrestrial carnivore, where mothers must accelerate rapidly to chase prey but, unlike many carnivores, they do not cache their offspring. Thus, proximity to the infant is repeatedly compromised during the mother's hunting, producing a trade-off between resource acquisition and maternal vigilance. Dietary differences between pregnant and lactating spotted dolphins (*Stenella attenuata*) suggest that lactating mothers may resist diving for more favorable prey (squid), and feed on the less desirable flying fish in order to stay near the surface with their vulnerable offspring who are less competent divers (Bernard and Hohn, 1989).

Bottlenose dolphin life histories, including long-term continuous contact with and care by the mother, a prolonged juvenile period, large brain size, long-term bonds, complex alliances, and a fission-fusion social organization, are patterns similar to those of the anthropoid primates, especially chimpanzees (see Smolker et al. 1992; Connor et al. 1992a, b; Goodall 1986; Smuts et al. 1987;

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Wrangham and Smuts 1980). Given the complexities of delphinid ecology, social structure, and life history, selection must favor developmental programs that enable the newborn to negotiate some tasks rapidly, while other skills develop slowly over the infancy and juvenile periods. Identifying the critical features of development (swimming, breathing, diving, hunting, socializing) and how mother and infant coordinate their behavior and associations, may help us understand what selective pressures favored delayed maturation and complex cognitive abilities in delphinids and the significance of individual variation.

INDIVIDUAL DIFFERENCES

Primate studies of individual differences tend to focus on either the mother (maternal style) or the infant (temperament and personality). Some studies, such as those of captive rhesus macaques (Suomi 1987, Higley et al. 1992, Clarke and Boinski 1995) and human attachment (Kagan et al. 1988, Belsky and Rovine 1987, Mangelsdorf et al. 1990) tend to focus on the interactions between infant characteristics and maternal style and personality. Because of the difficulty in assessing infant characteristics in naturalistic settings—that is, infants must be separated from their mothers to be tested on their reactions to novelty independent of the mother—field studies rarely attempt to disentangle maternal vs. infant contributions to infant behavioral development. Further, since primate mothers physically control infant contact and leave-taking, it is not surprising that maternal style is the focus of field studies and that maternal style is typically characterized as restrictive vs. laissez-faire (Altmann 1980), or protective vs. rejecting (e.g., Struhsaker 1971, Berman 1990). In addition to studies of individual variation in maternal style, some studies have identified species-typical patterns of maternal style among closely related species. For example, Maestriperi (1994) contrasted maternal style in three species of macaques. Species-typical differences in maternal style are consistent with the larger social patterns. For example, although all macaques live in female-bonded, matriline-based groups, rhesus macaque females tend to harass females of other matrilines and their infants, whereas pigtail macaque females are tolerant and friendly towards offspring of other females. Thus, pigtail mothers may be more laissez-faire with infants compared to rhesus monkey mothers (Maestriperi 1994). Species-level patterns and

individual patterns reflect the social and ecological environments that animals occupy.

Dolphins provide an interesting contrast with primates because of the dolphin infant's locomotor independence and apparent self-determination in where to go, when to go, and who to go with. Mothers do not appear to restrict their young, although they are likely to influence the behavior of their young. The infant tends to become separated from his mother when she hunts, providing the infant with the options of following her or exploring independently. Although it is difficult to tell, the infant appears to have the responsibility of monitoring the mother's whereabouts. This is not an easy task because the mother is not likely to be visible to the infant when she swims a mere five meters away. The primate's world is primarily a visual one, but the dolphin's world may be primarily acoustic. We are currently initiating a detailed study of mother-calf communication to determine exactly how mother and calf use whistles to negotiate separations and reunions and which member of the pair is responsible for increasing and/or decreasing proximity. This has particular relevance to the question of individual differences because one of the unusual features of bottlenose dolphins that distinguishes them from all nonmarine mammals, save humans and perhaps bats, is the development of individually distinctive vocal signatures, called "signature whistles."

VOCAL SIGNATURES

The bottlenose dolphin's elaborate communication system includes complex vocal learning, long-term acoustic memory, individual signatures, and sonar (Janik and Slater 1997, Caldwell et al. 1990, and Nachtigall 1980). With the exception of humans, vocal learning, defined as vocalizations that become "modified in form as a result of experience with those of other individuals" is absent among primates and most nonmarine mammals (Janik and Slater 1997, 59). These features evolved in the marine environment where visibility is low but sound transmission is efficient. It is under these conditions that dolphin mothers and infants must coordinate their activities, sometimes over hundreds of meters. Although mothers and infants appear to be capable of monitoring each other over long distances, the mechanisms involved are not known. Their communication system includes individual specific signature and nonsignature whistles

(Caldwell and Caldwell 1965; Caldwell, Caldwell and Tyack 1990; Sayigh et al. 1990, 1995), burst-pulsed sounds, and echolocation clicks (Popper 1980). Signature whistles may be defined as the predominant whistle type of an individual that is typically not shared by others (Caldwell et al. 1990). Aside from echolocation, only one study (Smolker, Mann, and Smuts 1993) examined the use of individual dolphin vocalizations under natural conditions. In this study, we demonstrated the use of whistles during mother-infant separations but were unable to identify unequivocally whether the mother or infant was whistling.

The signature whistle may be critical to the success of joining and leaving others in a fission-fusion society, a pattern that mothers and infants simulate in the early days of infancy. Given the fission-fusion social system in the marine environment, natural selection would have favored the evolution of signals that indicate identity and location of the caller. However, some basic questions remain. If the benefits of a fission-fusion social system allow individuals to maintain social contacts, but maximally exploit fish distributions, do infants and mothers equally benefit from separations? Why do infants and mothers separate at all? Second, given that they do separate, why do some infants tend to swim far from their mothers often and others tend to stay close? Finally, what are the costs of separations in terms of maternal and infant survivorship and reproduction? Individual differences may have implications for infant development and maternal or infant reproductive success.

EARLY DEVELOPMENTAL PATTERNS IN MOTHER-INFANT PROXIMITY

Newborn dolphins, although capable and rapid swimmers, must solve several problems quickly, such as breathing (which is voluntary and occurs irregularly), diving, and staying with the mother. One way to solve these problems is to follow and synchronize breathing with the mother, a pattern evident in the echelon formation swimming (close parallel swimming) of wild bottlenose dolphin newborns and high degree of breathing synchrony (Mann and Smuts, in press-b). Several studies of captive *Tursiops* have also reported echelon swimming in newborns (e.g., Reiss 1988, Cockcroft and Ross 1990, Eastcott and Dickinson 1987, Tavolga and Essapian 1957, Reid et al. 1995). In

the wild, echelon swimming declines rapidly in the first few weeks of life, but for some infants, continued into the second month of life (Mann and Smuts, in press-b). Norris and Prescott (1961) proposed that infants receive a hydrodynamic boost by swimming echelon, but the possibility of such energetic benefits awaits quantification.

By the end of the first month, infants swim in infant position (under the mother, with the melon lightly touching her abdomen) (Cockcroft and Ross 1990, Mann and Smuts, in press-b). After the newborn period, they maintain this contact position roughly twenty to fifty percent of the time until weaning (Mann and Smuts 1993). Little is known about the possible hydrodynamic benefits of infant position swimming or the energetic costs this position may carry for the mother.

Consistent with captive studies of proximity maintenance in *Tursiops* (Reid et al. 1995) and of free-ranging right whales (Taber and Thomas 1982), we found a decline in the mother's responsibility in maintaining proximity to her infant in a wild population (Mann and Smuts, in press-b). Although calves did the majority of approaches and leaves, mothers were typically more likely to approach than leave their calves throughout the newborn period (defined here as the first three months of life).

INDIVIDUAL VARIATION: EXAMPLES AND IMPLICATIONS

In 1988, Barbara Smuts and I initiated a longitudinal study of bottlenose dolphin mothers and calves in Shark Bay, Western Australia. In Shark Bay, a team of researchers has been studying the behavioral, reproductive, demographic, and ecological characteristics of a population of wild bottlenose dolphins (over 600 animals), *Tursiops truncatus*, since 1984 (Connor and Smolker 1985). This resident population is well-habituated to small boats, enabling observers to stay with individual dolphins all day. Each mother-calf pair is observed for ten to twenty hours annually during a three to four month field season from birth to one year after weaning. I present here a subset (approximately one third) of our longitudinal database on twelve of the thirty-six infants we have studied. The total observation time for these twelve infants was 427 hours. The newborn period (first three months) was excluded from these analyses. Not all infants were observed in all years. Continuous and instantaneous samples (Altmann 1974) on

mother-infant proximity and activity were systematically noted during focal-infant follows. These results are preliminary. Further analyses with the complete dataset may yield different results.

Figures 1 and 2 show the proportion of time that different infants swim in infant position (contact) with the mother from the first year of life to the second year of life (Figure 1), and from the second year of life to the third year of life (Figure 2). Instead of showing a decline from year to year, a pattern predicted by Trivers' theory of parental investment (1972, 1974) and typical of most mammals (e.g., baboons, Altmann 1980; rhesus monkeys, Berman 1980; red deer, Clutton-Brock et al. 1982; fur seals, Trillmich 1986), infants actually significantly *increased* the time spent in infant position from the first to the second year (Wilcoxon Matched Pairs Signed Ranks Test, $p < .03$, $N=9$), but showed no change from the second to the third year. The average percent time spent in infant position was 30.1% ($SD=8.3$) during the first year, 36.2% ($SD=13.1$) during the second year, and 37.9% ($SD=8.8$) during the third year.

Figures 3 and 4 show the proportion of time infants spend away from their mothers, defined here as greater than twenty meters. Infant variability is more apparent here, with some infants spending less than three percent of their time away from their mothers and others spending over forty percent of their time away. The time spent away from the mother does tend to increase from the second year to the third year of life (Matched Pairs

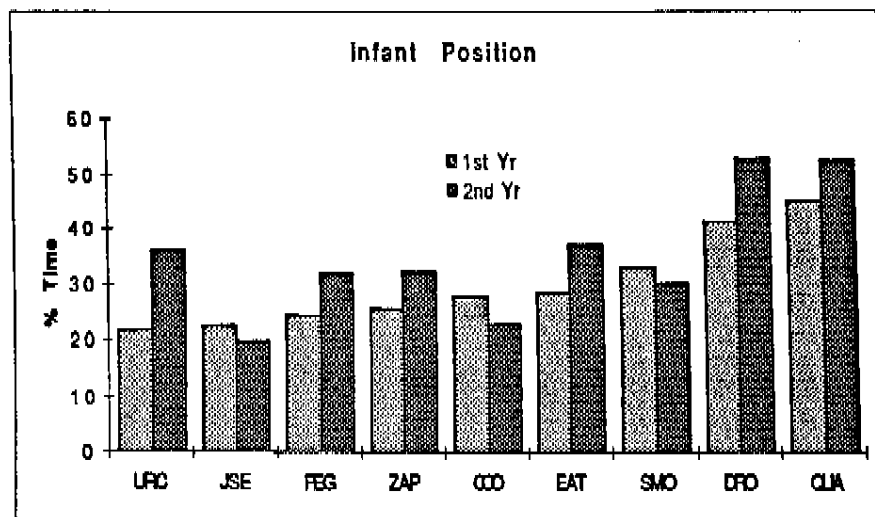


Figure 1. Significantly increased time spent in infant position from the first to the second year of life (Wilcoxon Matched Pairs Signed Ranks Test, $p < .03$).

Signed Ranks Test, $N=7$, $p<.06$). Individual variation is higher for time away from the mother than for time in infant position. The average percent time spent more than twenty meters from the mother was 13.9% ($SD=9.0$) during the first year, 18.0% ($SD=15.7$) during the second year, and 25.0% ($SD=12.5$) during the third year. Note that the standard deviations are much larger for time away than for infant position.

Time away from the mother could have implications for the infant's social and hunting or foraging experience. Infants who strayed from their mothers tended to explore. Treating each infant year as independent, the time spent away ($>20m$) from the mother is significantly correlated with time the infant spends socializing and/or foraging (Spearman's $r = 0.73$, $p<.001$, $N=27$ infant years), and negatively correlated with the time the infant is either in contact with the mother (Spearman's $r = -0.57$, $p<.005$, $N=27$ infant years), or not in contact but less than twenty meters from her (Spearman's $r = -0.42$, $p<.05$, $N=27$ infant years). If socializing and foraging are examined separately, the correlations remain significant. This is not surprising since roughly eighty percent of the time infants are greater than twenty meters from their mothers, they are most likely foraging and, if not foraging, socializing (Mann and Smuts 1993). Thus, infants who leave their mothers are more likely to gain foraging and socializing experience.

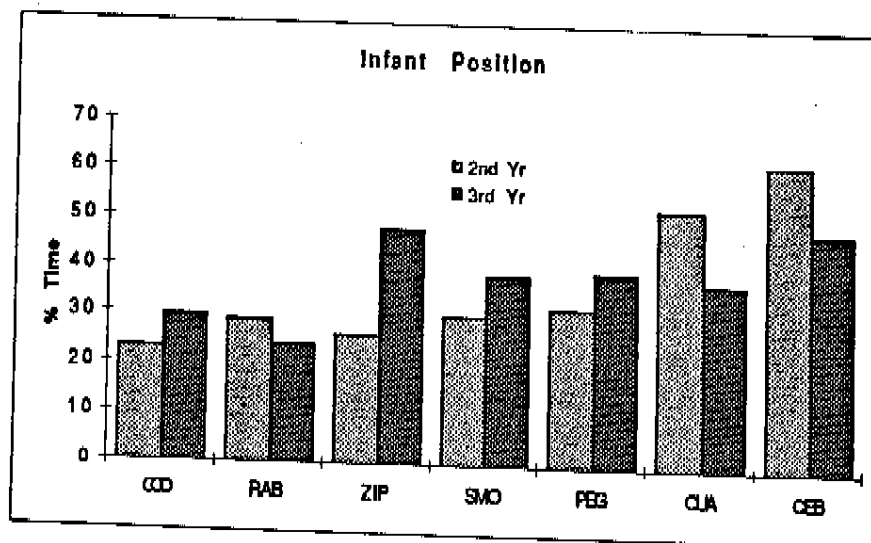


Figure 2. Infants showed no change in time spent in infant position from the second to third year of life. Wilcoxon Matched Pairs Signed Ranks Test, NS.

SOCIAL DEVELOPMENT

Infants engage in a wide variety of social interactions with many different social partners. Most often their social partner is the mother or another immature (Mann and Smuts, in press-a; Mann unpublished data). Inexperienced females (immature females and those who lost infants in the first few months of life) and other infants are very attracted to newborns and, besides the mother, tend to be their social partners during the first months of life. Adult males virtually never associate with infants (Mann and Smuts, in press-a). Social activities include chasing, mounting, rubbing, contact swimming, petting (moving the pectoral fin on the body part of another), and a variety of displays (belly, face, and tail slaps, leaps, spy hops, etc.). Newborn play is characterized by chasing and displays, and involves very little body-to-body contact (Mann and Smuts, in press-b). This appears to be different from play of older infants, which tends to involve extensive contact. Petting and rubbing is a common affiliative behavior across all age and sex classes. We consider this behavior analogous to primate grooming, with modest hygienic, but predominantly social functions. Aggressive behavior very rarely involves infants.

Socio-sexual behavior occurs at early ages in delphinids, but systematic observations are lacking and adaptive significance is not well understood. Haenal (1986) reports that penile erections are common among wild killer whale infants, but ages are not specified. Erections are also common among bottlenose

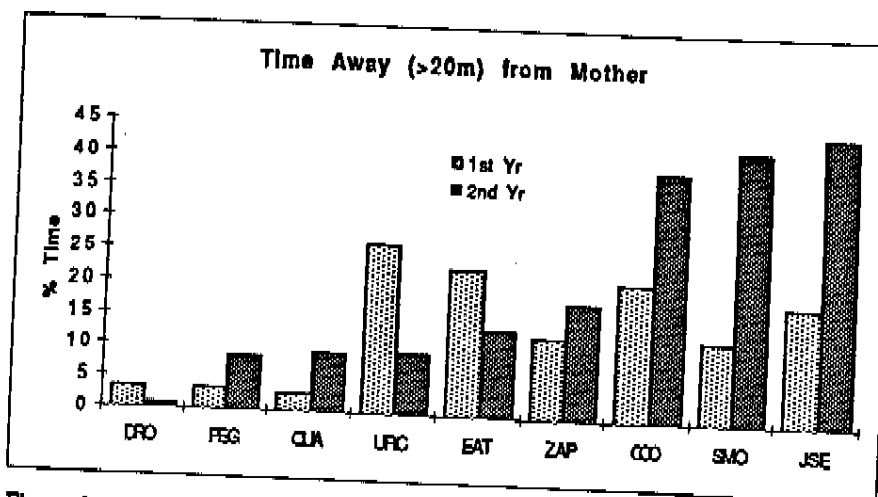


Figure 3. Infants showed no change in time spent >20m from the mother from the first to second year of life. Wilcoxon Matched Pairs Signed Ranks Test, NS.

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FALL 1997

VOL. 4, No. 1

INDIVIDUAL DIFFERENCES IN BOTTLENOSE DOLPHIN INFANTS

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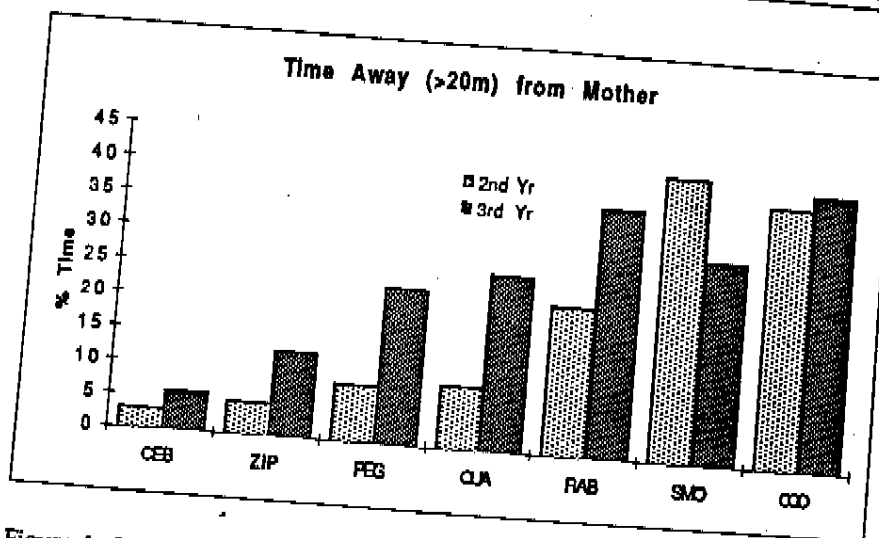


Figure 4. Infants tended to increase time spent >20m from the mother from the second to third year of life. Wilcoxon Matched Pairs Signed Ranks Test, $p < .06$.

dolphins, beginning in the newborn period (Mann and Smuts, in press-b), but are not common until the calf is older. Calves frequently engage in a specific type of triadic play, which we have dubbed "play herding" because of its similarity to adult male herding described by Connor and his colleagues (Connor et al. 1992a, b). Adult males form long-term alliances of pairs or triplets that cooperate to aggressively herd adult females. Infant males seem to take up this practice in "play" by joining one or two other males to swim behind, display at, and attempt to mount a third animal, who may be male or female. Since both sexes have a genital slit, intromission is possible with both sexes. Females of any age rarely mount males and virtually never position themselves in formation behind males or females during "play herding." If play herding involves three or more males, then role switching is common where one of the "mounters" may become the "mounee."

FORAGING

In aquaria, bottlenose dolphin calves typically take fish between six and twelve months of age (Essapian 1953, Amundin 1986, Caldwell and Caldwell 1972, Cockcroft and Ross 1990). Shark Bay calves have been observed practice hunting during the newborn period and catching small fish between four to six months of age, but not earlier. The first three months appear to

be devoted to "practice" hunting, which begins by the second month, but can occur as early as the end of the third week. In the newborn period, hunting-like behaviors are the last to appear of all other behavior categories, and some infants were not observed "play hunting" at all during the first two months of life. Shark Bay infants have a characteristic hunting style that we call "snacking." During snacking, the infant swims belly-up near the surface and traps small fish at the water surface. Young infants are seen to repeatedly chase and snap up a piece of sea grass. Infants show a steady increase in the proportion of time foraging as they age (Mann and Smuts 1993).

CONCLUSIONS

The preliminary results shown here illustrate the paradox alluded to earlier, increasing independence while maintaining dependence on the mother for the first few years of life. The apparent benefit of mother-infant separations is that the infant gains more social and foraging experience. The mother may also benefit by being able to hunt more efficiently without an infant in the way. If some infants benefit from frequent leave-taking, what are the costs? Infants who spend more time away from the mother are spending less time in infant position (Spearman $r = -0.65$, $p < .005$, $N = 27$ infant years), and so may nurse less often. Infants may also be more vulnerable to becoming lost, separated, stranded, or preyed upon when separated from the mother. Risk of aggression by conspecifics towards infants does not appear to be a risk (as it is in many primate species). Infants who separate often from the mother may gain benefits after weaning because they would have adequate hunting and social experience to guide them through independence, but they might suffer higher mortality risk during infancy. In contrast, infants who remained close to their mothers might have lower mortality risk during infancy but be more vulnerable when they were independent because of their relative lack of experience. Preliminary analyses of mortality risk suggest that this is not the case. Infants who stay close to their mothers are not more likely to survive to weaning than those who stray (Mann and Smuts 1994). There may be other factors involved, such as the varying social and ecological conditions that mothers and infants live with.

Although dolphins differ in many ways from terrestrial mammals, some similarities in maternal care and infant develop-

ment are striking. Maternal style is difficult to separate from infant behavior, but the variation in infant behavior appears to fall along the bold-shy or inhibited-disinhibited dimension found in primate studies of temperament, maternal style, and attachment. This basic orientation reflects differing behavioral strategies although the costs and benefits of these strategies are not well understood. Why does the pattern of contact, infant position swimming, not decline over time and, in fact, increase from the first to the second year? While locomotion and carrying infants is very costly in primates (e.g., Altmann and Samuels 1992), the locomotion costs for dolphins are relatively small (Williams et al. 1993) and, perhaps, any costs to the mother associated with infant position swimming are small enough that she can tolerate this form of contact swimming until weaning. Although mothers may tolerate infant position swimming, they may be less tolerant of nursing as the infant ages. We cannot test this hypothesis easily with wild dolphins because the rate of nursing can only be determined with continuous underwater observations. Although infants vary little in the time spent in infant position, they do vary considerably in the degree to which they stray from their mothers. Like foraging and the development of social bonds, learning to leave and rejoin the mother is a critical skill for the infant to master in a fission-fusion society. Sex of infant, habitat differences, and parity and sociability of the mother are likely to relate to these individual differences and the consequences thereof. By following these infants into adulthood, we hope to gain further insights into the adaptive significance of this variability. *

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ALL 1997

VOL. 4, NO. 1

INDIVIDUAL DIFFERENCES IN BOTTLENOSE DOLPHIN INFANTS

47

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