

Synchrony between a Mother-Calf Pair of Bottlenose Dolphins (*Tursiops truncatus*)

by

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Abstract

Behavioral synchrony is a phenomenon that has been observed in dolphins, but the behavior has yet to be quantified. Dolphins behave synchronously while travelling, foraging, resting, playing, mating, and as a fear response. Through microanalysis of videotapes, the current study examined the ontogeny of synchrony between a bottlenose dolphin and her newborn calf during the first 4 weeks of life. The pair maintained synchrony 97.7% of the time. The most common formation was touching trunk-to-trunk in echelon position. Suckling was first observed at 16 hrs of age and was associated with a period of increased chaos. Once suckling was established, higher levels of synchrony resumed, and the calf attained more freedom. It is theorized that milk is a reinforcer for synchronous behavior. Several functions of synchrony are proposed including energy conservation, increased vigilance, predator avoidance, and communication.

Dedication

For continually providing inspiration and opportunities for contemplation of non-human perspectives, I dedicate this work to Noriko and Naia, my Nina, Ally, and in memory of Max.

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Synchrony between a Mother-Calf Pair of Bottlenose Dolphins (*Tursiops truncatus*)

Synchronous behavior among dolphins is an often-mentioned but rarely studied phenomenon. Bottlenose dolphins have been observed moving in synchrony with each other while travelling and while foraging or feeding (Bel'kovich, 1991). Descriptions of coordinated hunting efforts reported by Saayman, Tayler, & Bower (1973; *Tursiops aduncus*) also suggest a high degree of synchrony. Several observers have noted that at least two genera of dolphins form a cohesive, synchronous school as a fear reaction in response to predators, novel objects, and novel situations (*Tursiops truncatus*: Bel'kovich, 1991; McBride & Hebb, 1948; Tavolga, 1966; *Stenella longirostris*: Johnson & Norris, 1994; Norris & Johnson, 1994; *Stenella attenuata*: Pryor & Shallenberger, 1991; Norris & Dohl, 1980). Johnson and Norris (1994) observed a mother spinner dolphin (*Stenella longirostris*) that appeared to be teaching her calf how to perform aerial behaviors by leaping synchronously with it. Male dyads or subgroups are often reported to move in synchrony with each other (Pryor & Shallenberger, 1991), especially during herding or mating encounters (Connor, Smolker, & Richards, 1992; Saayman, Tayler, & Bower, 1973). Bottlenose dolphins often move synchronously while rubbing or caressing each other (Johnson & Norris, 1994; Saayman, Tayler, & Bower, 1973). In both bottlenose and spinner dolphins, synchrony is evident during play episodes between both adults and juveniles (Bel'kovich, 1991; Johnson & Norris, 1994).

Although synchrony is pervasive in many qualitative descriptions of cetacean behavior, it is an activity that the scientific community knows little about. In order to begin to elucidate why dolphins tend to behave synchronously, it may be helpful to first examine synchrony in other species.

Schooling in Fish and Flocking in Birds

The behaviors of schooling fish and flocking birds share many similarities. Several investigations of the mechanisms of schooling and flocking parallel each other and also share several hypotheses as to why schooling and flocking are beneficial.

Birds or fish that move in a similar orientation to each other with regular spacing and uniform speed can be classified as “polarized” (Breder, 1967; Partridge, 1982a). Non-polarized groupings are called aggregations, and aggregations of fish are often called shoals to differentiate them from a polarized school. Aggregations will sometimes become polarized briefly, but generally have a loosely organized structure. The use of computer simulations has shed considerable light on the mechanisms of polarized movement. The movement of polarized groups appears to be governed by local rules that apply to each individual. A member’s position within the group reflects a compromise between local rules of attraction and repulsion, that is, attraction to the safety of the group and repulsion from being too close to neighbors. In addition, each member matches its velocity and heading to the average of its nearest neighbors (Aoki, 1982; Hasegawa &

Soeda, 1985; Heppner & Grenander, 1990; Lawren, 1991; Niwa, H.-S., 1996; Vabø & Nøttestad, 1997; Wickelgren, 1990).

In fish, the ability to school develops at about the time of metamorphosis from the larval to the juvenile stage in Atlantic herring (*Clupea harengus*; 35-40 mm; Gallego & Heath, 1994). More specifically, Masuda and Tsukamoto (1998) found that the ontogeny of schooling was dependent upon development of the visual systems in striped jack (*Pseudocaranx dentex*; 12 mm or 25 d).

As suggested by Masuda and Tsukamoto, schooling is primarily mediated by vision, and secondarily by mechanosenses. In experiments with coho salmon (*Oncorhynchus kisutch*) in which light intensity was gradually reduced, it was found that lower levels of light caused greater nearest neighbor distances (NND) and nearest neighbor angles (NNA), two variables used to quantify degree of polarity (Azuma & Iwata, 1994). Similarly, Hunter (1969) found that a jack mackerel (*Trachurus symmetricus*) stimulated by shock and positioned parallel to a response fish had a greater impact on the response fish's velocity than a stimulated fish positioned either in front of or behind the response fish. Hunter theorized that the lateral fish occupied more degrees of arc in the visual field and so was better seen and had more of an impact on the response fish. The degree of the response also relied upon the angle of velocity, and therefore on the visual perception of movement. Light reflecting off of external surfaces

(including the lateral line) of the horse mackerel (*Trachurus trachurus*) helps neighbors to keep track of each other's velocity and direction (Rowe & Denton, 1997).

Although vision is important for schooling, Pitcher, Partridge, and Wardle (1976) found that a blinded saith (*Pollachius virens*) was still able to school, although its NND was significantly greater than before it was disabled. This suggests that it is specifically the rules of attraction that are dependent upon the sense of vision. When the lateral line of golden shiners (*Notemigonus crysoleucus*) are denervated, NND becomes smaller, suggesting that the rules of repulsion are dependent upon mechanosenses (Burgess & Shaw, 1981). Based on a series of experiments in which fish were either blinded or their lateral lines denervated, Partridge and Pitcher (1980) also maintain that vision is primarily important for the maintenance of position and angle between fish, and the lateral line is primarily important for monitoring the swimming speed and direction of travel of neighbors (see Partridge, 1981, 1982b for reviews).

The ontogeny of flocking has not been reported. Presumably, the ability to move in a coordinated flock is mediated primarily by vision, although auditory cues and subtle changes in the airstream cannot be discounted. Potts (1984) has suggested that synchronized movement is enhanced by a "chorus line" effect. After analyzing flocks of dunlin (*Calidris alpina*), Potts concluded that a single member was able to initiate a maneuver. The initiator's nearest neighbors responded with a speed that was slower than experimentally observed minimum reaction times, as expected. As the movement spread

throughout the flock, however, reaction times between neighbors decreased until they became up to three times as fast as minimum reaction time. This suggests that individuals monitor movements of distant flock members and are therefore able to anticipate rapid turns or swoops with a response time that would be impossible if they were only watching their nearest neighbor.

Several possible functions of schools and flocks are currently under investigation, but they may be broken into three main categories: energy conservation, increased vigilance, and directly decreasing the risk of predation through confusion and dilution effects.

Energy Conservation. Breder (1965) and Weihs (1973, 1975) have proposed that theoretically, energy conservation may be a primary function of schooling.

Experimentally, energetic savings by schooling have been found in sea bass (*Dicentrarchus labrax*; Herskin & Steffensen, 1998) and in the golden shiner (*Notemigonus crysoleucas*; Boyd & Parsons, 1998). The tailbeat frequency and oxygen consumption rates of sea bass indicated a 9-23% energetic savings in schooling fish over solitary fish. However, this is far short of the 40-50% savings predicted by Weihs.

Likewise, golden shiners demonstrated more endurance while schooling than when swimming alone, but their positions did not conform to predicted optimal configurations. (Interestingly, when fish were partitioned away from each other with either a clear or an opaque divider, those that were in visual contact with each other had greater endurance

than those that were visually isolated, suggesting that schooling may also have a calming, and therefore energy-reducing, effect in and of itself.) It appears as though some energetic savings are realized by schooling fish, but that the savings may be incidental and that other functions may take precedence (Abrahams & Colgan, 1985; Nonacs, Smith, & Mangel, 1998; Parrish, 1988).

Mathematical models have also been developed that predict energy conservation in flocking, particularly in species that fly in a “V” formation (Cutts & Speakman, 1994; Lissaman & Schollenberger, 1970). However, direct observation has failed to demonstrate that either pink-footed geese (*Anser brachyrhynchus*; Cutts & Speakman, 1994) or Canadian geese (*Branta canadensis*; May, 1979) fly in the ideal positions to realize the potential energy savings. Similar attempts to discover energy savings in polarized flocks that do not fly in “V” formations have demonstrated that energy conservation is not a likely primary function of flocking (Higdon & Corrsin, 1978; Pomeroy & Heppner, 1992).

Increased Vigilance. At the core of the increased vigilance or “many eyes” hypothesis is the idea that being in a group results in a heightened awareness of the group’s surroundings over the awareness of any single individual. The first implication of this heightened awareness is an improved chance of finding food. The second implication is that the group will potentially have an earlier warning of impending predation. The

collective awareness of a group is dependent upon a method of communication between a member and the group as a whole.

As predicted by the model, schooling fish are more successful foragers than single fish, and the success rate increases linearly with school size (Pitcher & Parrish, 1993).

Shoaling, or non-polarized aggregating by fish, has been shown to facilitate learning.

Laland and Williams (1997) found that after training a group of guppies to follow one of two routes to food and then putting untrained guppies in with them, the untrained guppies followed the same path as the trained guppies even though following the alternate path was equally likely to lead them to food. After the trained guppies were removed, the untrained guppies continued to follow the same path as the trained guppies. The tradition of following a specific path was transmitted to the untrained schoolmates. Similar results were found in a transplanted group of free-ranging coral reef fish that learned to follow an established daily migration route by following experienced, resident fish (Helfman & Schultz, 1984).

Although schools are generally considered to be leaderless, under the right circumstances, a single individual can direct the rest of the school. Romey (1996) created a computer simulation that included “biased” fish that were programmed to have a preference for moving in a particular direction. It was discovered that a fish that moved with purpose was capable of altering the direction of the school as a whole. Although it was shown that the biased fish influenced the movement of the school, observers of the

simulated school could not discern which was the “leader.” Experimental observations have also demonstrated that when one fish has relevant information that the rest of the school members do not have, whether it is immediate sensory information or a learned response, the knowledgeable fish will deviate from the school’s average heading and velocity in order to react to the information. The other members of the school will then respond to the deviant fish by adjusting their behavior to match the new average (*Aphyocharax* sp.: Levín, 1996; Vergara & Levín, 1982; *Hemigrammus caudovittatus*: Zhuikov & Pyanov, 1993). In some species, however the knowledgeable fish’s ability to act on its knowledge will be compromised if the unknowledgeable school members are alarmed because of an overriding attraction to the school (*Cyprinus carpio*: Köhler, 1976; *Oncorhynchus keta*: Ryer & Olla, 1991).

Birds also can benefit from foraging in groups rather than alone, but the advantage does not necessarily require synchronous or polarized movement. One line of evidence to support increased foraging efficiency comes from mixed-species flocks. It has been shown that when one of two mixed-species flocks are provisioned, only the non-provisioned flock continues to forage together. Instances of mixed-species flocking by the provisioned birds diminish (Berner & Grubb, 1985; Grubb, 1987). This suggests that it was the increased foraging efficiency that caused the birds to flock together. Another situation in which flocking boosts foraging performance is when unsuccessful foragers follow successful foragers to food. Common terns (*Sterna hirundo*) were observed

leaving their communal roost, and the observers followed them to feeding locations.

Birds that left the roost together generally flew to the same feeding area and were more successful than those that foraged alone. When an individual returned to the roost with a fish, that bird was more likely to be followed on its next outing. Terns that were unsuccessful in finding food were consequently more likely to follow other birds than to strike out alone a second time (Waltz, 1987). Similar results have been observed in several other species (see Ward & Zahavi, 1973 for a review).

The main difference between non-polarized aggregations of fish and birds and polarized schools and flocks with regard to information transfer appears to be the speed with which the information is transferred. Whereas information transfer in non-polarized groups is normally described over a period of hours or days, information transmitted in polarized groups is nearly instantaneous. When it comes to avoiding predators, time is of the essence. One of the benefits of having “many eyes” to watch for predators is that the chances of early detection are increased while simultaneously freeing individuals to devote more of their attention to other activities, such as feeding.

There is evidence to suggest that group membership provides benefits in the form of enhanced detection and avoidance of predators. One study showed that fish are more likely to school when there are no landmarks or protective structures because schooling provides a “pseudo-shelter” which allows safer exploration of the environment (Mikheev, 1995). Both minnows (*Phoxinus phoxinus*) and salmon (*Oncorhynchus keta*) are capable

of receiving and responding to alarm responses displayed by their schoolmates (Magurran & Higham, 1988; Ryer & Olla, 1991). The escape behavior of schooling herring (*Clupea harengus*) is more accurate than a solitary herring because the school is able to integrate sensory information from the movements of startled neighbors (Domenici & Batty, 1997). There is also a preference for fish to school with familiar fish which bestows an advantage because fish that are familiar with each other demonstrate better predator avoidance behavior (Griffiths, 1997). Sticklebacks (*Gasterosteus aculeatus*) have even been shown to receive information about danger when chubs (*Leuciscus cephalus*) respond to an alarm chemical to which sticklebacks are insensitive, demonstrating intraspecies information transfer (Krause, 1993).

Larger flocks of birds also benefit from the increased vigilance afforded by having “many eyes” (Pulliam, 1973). In house sparrows (*Passer domesticus*), an inverse relationship was found between flock size and time spent in predator surveillance (Elgar & Catterall, 1981). Similar results were found with red-billed weaverbirds (*Quelea quelea*) in which decreased amounts of individual vigilance led to increases in the amount of food consumed (Lazarus, 1979b). Lazarus (1979a) also found that as flock size increased the type of response elicited by a predator changed from the more extreme response of taking wing, to flight intention movements, to a more conservative response of orienting towards the predator. This trend can be understood functionally in terms of the reduced risk of capture in larger flocks. Some species (turnstones, *Arenaria interpres*,

and purple sandpipers, *Calidris maritima*) will even exhibit decreased levels of individual vigilance while in mixed-species flocks, again demonstrating intraspecies information transfer (Metcalf, 1984).

Decreased risk of predation. In addition to facilitating predator detection among its members, schooling and flocking behavior can reduce a predatory attack's effectiveness directly through dilution and confusion effects. A dilution effect occurs when an individual's chance of being attacked decreases linearly with the size of the group. That is, each individual's probability of being selected as a target is reduced when there are 50 fish to choose from rather than 5. A confusion effect occurs when the predator has difficulty zeroing in on any one member because of the simultaneous movement of all members of the group. Partridge (1981, 1982b) has proposed that protection against predation via dilution and confusion effects is the primary purpose of schooling.

Roberts (1996) has similarly argued that reduced predation is primarily responsible for flocking in birds, pointing out that the decreased amount of vigilance that is attributed to the "many eyes" hypothesis may actually be the indirect result of decreased pressure to be vigilant because each individual is actually safer. This argument appears to have some merit as spotted turtle doves (*Streptopelia chinensis*) were shown to reduce their vigilance while feeding at square feeders but not while feeding at linear feeders, presumably because each individual bird felt less at risk while clumped together

(Sadedin & Elgar, 1998). Cresswell (1994) reported that although predators attacked large flocks of redshanks (*Tringa totanus*) more often, attacks on smaller flocks were more likely to be successful. House sparrows (*Passer domesticus*) prefer to join larger flocks than to forage alone or in pairs, even when this decision reduces food intake (Elgar, 1987).

In summary, although energy conservation at first appeared to be a likely function of synchronous behavior, the experimental evidence failed to demonstrate anything near optimum energy savings. Secondly, the predictions of the “many eyes” hypothesis are consistent with observations of large groups. Although synchronous behavior is not necessary for the transmission of information, particularly in the case of foraging, synchrony may be helpful for rapidly transmitting signals between members. Thirdly, the decreased risk of predation has strong support in the literature and also fits nicely as a function of synchrony. Both dilution and confusion effects are optimized when all members look or act similarly.

Thus far, there appear to be some similarities and some differences in how synchronous movements are used in fish and birds as compared to dolphins. Both groups potentially benefit while travelling, foraging, feeding, and avoiding predators because of the possible conservation of energy, transmission of relevant information, and dilution and confusion effects. Although both vocal and motor imitation have been observed in some birds (Moore, 1996), the role of imitation in flocking formations is not clear. In

addition, a thorough search did not turn up any evidence of imitation, teaching, or play in fishes.

Flashing in Fireflies

Another striking example of synchrony occurs in the insect world. There is a very interesting phenomenon in some species of fireflies that inhabit parts of Southeast Asia. Along certain riverbanks in Thailand, Malaysia, and New Guinea, millions of male fireflies congregate in the trees flashing in perfect synchrony, their rhythm more regular than a sleeping human's heartbeat (Buck, 1988). In the 1930s, biologist Hugh M. Smith described the effect vividly:

Imagine a tree thirty-five to forty feet high . . . apparently with a firefly on every leaf and all the fireflies flashing in perfect unison at the rate of about three times in two seconds, the tree being in complete darkness between flashes. . . . Imagine a tenth of a mile of river front with an unbroken line of trees with fireflies on every leaf flashing in synchronism, the insects on the trees at the ends of the line acting in perfect unison with those between. Then, if one's imagination is sufficiently vivid, he may form some conception of this amazing spectacle.

(Stewart, 1999, p. 104)

Each firefly's flash is controlled by a neural timing mechanism in the brain that can be influenced by photic stimulation of the eye. The timing mechanism is best described as a pulse oscillator that regulates the amount of time that must elapse before the next flash. The period between flashes is species specific and is accurate to about 13 msec in the New Guinea firefly (*Pteroptyx cribellata*). The timer operates much like the action potential of a neuron in which a charge gradually builds until a specific threshold is reached, the system discharges in the form a flash, and then the charge returns to baseline (Hanson, Case, Buck, & Buck, 1971).

Witnessing a neighbor's flash can either cause the oscillator's charge to increase, called phase-advanced, or cause the oscillator to reset itself without discharging and start the count over, called phase-delayed. The tendency to exhibit phase-delayed or phase-advanced behavior also appears to be species specific, although more research is needed to confirm that each species is exclusively of one type or the other (Buck, 1988).

In phase-delayed species, the flashing of Firefly B next to Firefly A resets A's oscillating timer so that on the next cycle, both will flash together (Buck, 1988). Once entrained, the two will continue to flash synchronously indefinitely because their species-specific oscillators are set to the same phase length. In phase-advanced species, the sensitivity of the oscillating timer to other flashes is the key to coordinating the flashes of the entire population. According to the Mirollo-Strogatz model, each oscillator is coupled to every other oscillator within the firefly's visual field. When Firefly B flashes next to

Firefly A, it causes A's oscillating timer to advance prematurely until, after a few cycles of flashes, A will become entrained to B's rhythm. In both phase-advance and phase-delayed species, A and B will then have a similar effect on their neighbors until each individual is absorbed into A and B's rhythm (Stewart, 1991; Strogatz & Stewart, 1993).

Although progress has been made in determining the mechanisms of synchronous flashing, the function of this population-wide synchrony is still unknown. One speculation is that synchronous flashing affords increased visibility from longer distances than if the flashes were temporally distributed. Flashing in synchrony could serve as a beacon to females who must travel through dense vegetation to find males with which to mate. Other possibilities include methods of identification of females (because they do not flash synchronously), or identification of conspecifics (Buck, 1988).

Although the mechanisms and outward manifestations of synchrony are most likely different between fireflies and cetaceans, this does not automatically preclude similarity of function. The specific message of the firefly's flash has not yet been decoded, but the purpose appears to be signaling of some kind. It is possible that synchrony in dolphins may also convey information to others.

Human Interaction

Synchrony has also been a subject of study in human behavior. What has generally been termed synchrony in the literature has alternatively been called

interactional synchrony, dyadic synchrony, perceived synchrony, mutuality, or social coordination. This type of synchrony, which includes both verbal and nonverbal behavior, is characterized by a smooth, rhythmic flow of interaction between dyad members, a fluid give-and-take, and joint attention to a single topic or object. From this point on, this type of synchrony will be termed social coordination in order to avoid confusion with simultaneous movement.

Various functions have been proposed for social coordination. Social coordination facilitates smooth verbal exchange, and can be a communication tool in and of itself by signaling interest and approval (Bernieri, Reznick, & Rosenthal, 1988). It also appears to be important in parent-child interactions. Mother-child coordination is higher when the child has a secure attachment style versus an insecure attachment style (Crandell, Fitzgerald, & Whipple, 1997; Isabella, Belsky & van Eye, 1989). Higher levels of coordination with parents during infancy or toddlerhood are associated with more incidences of symbolic play at two years of age (Feldman & Greenbaum, 1997), better adjustment in kindergarten (Harrist, Pettit, Dodge & Bates, 1994), and increased cognitive abilities at two and five years of age (Kirsh, Crnic & Greenberg, 1995). Social coordination is negatively correlated with having an alcoholic father (Whipple, Fitzgerald & Zucker, 1995).

Tronick, Als, and Brazelton (1980) described another method of measuring social coordination that has been useful with very young infants. Tronick et al. videotaped

mothers as they played face-to-face with their infants who were sitting in a car seat. The videotapes were then analyzed frame by frame for specific characteristics of gaze, head orientation, facial expression, and body position. Various combinations of those characteristics were distilled into seven monadic phases: avoid, avert, monitor, set, elicit, play, and talk. The critical feature of Tronick et al.'s system was whether the mother and infant were engaged in similar phases and whether they coordinated changes in phase with each other. Studies that use the face-to-face play paradigm have discovered that high levels of mother-infant coordination at three and nine months are associated with higher levels of self-control and symbolic play at two years (Feldman & Greenbaum, 1997; Feldman, Greenbaum & Yirmiya, 1999). There is some evidence to suggest that the infant's ability to maintain the rhythm of the interaction is biologically based in that pre-term infants exhibit less social coordination than full-term babies at both three and five months (Lester, Hoffman & Brazelton, 1985).

An interesting feature of social coordination is that members of the dyad often react to each other at speeds that are impossibly fast given the neurological limits of reaction times. Stern (1977) notes that typical interactions are generally perceived as a back-and-forth phenomenon where each partner reacts directly to the other partner's last action. However, this perception isn't supported by laboratory observation. Instead, it appears as if humans generally share a common program of expected rhythmic exchanges. When the partner's behavior deviates from the anticipated rhythm, the

deviation provides clues about what to expect on subsequent volleys. It is therefore not specific behaviors that trigger specific responses from a social partner, it is a pattern of behaviors that guide the course of smoothly-coordinated interaction. Stern provides an example of a couple dancing a waltz. Both partners have knowledge of the overall structure of the dance, but at specific, predetermined intervals, decisions must be made and effectively communicated to each other in order for the dance to continue smoothly. A couple with a high level of coordination will be able to negotiate these decision points effortlessly by using cues provided by what happened at the last decision point, and the one before that. If they were only using the information from the last step taken before the decision point, there would not be enough time to react appropriately, and coordination would suffer.

Another type of synchrony in humans is generally referred to as simultaneous or reciprocal imitation. The behavior begins with one person imitating another's action, but then both continue the behavior together synchronously. In some cases, the line between synchrony and imitation is difficult to distinguish as imitation could be described as delayed synchrony.

The ability to engage in complex acts of imitation first appears at about 18 months of age, which is also the same age as toddlers begin to develop a self concept. It is theorized that children are able to synchronize their movements with another because they have recognized themselves as a "self" and the other person as an "other" and can

now cause the Self's actions to correspond with the Other's actions (Asendorpf & Baudonnière, 1993; Asendorpf, Warkentin, & Baudonnière, 1996). Imitation quickly becomes a primary vehicle of communication for this age group. Once imitation begins to occur, its incidence increases until about 20-28 months of age when its use is superceded by verbal communication. At that point, the occurrence of imitation begins to decline (Baudonnière, 1988; Eckerman, Davis & Didow, 1989; Nadel-Brulfert & Baudonnière, 1982). Imitation is the most common response to a play overture performed by either an adult (Eckerman & Didow, 1989) or a peer (Ross, 1982). Likewise, when adults purposefully imitated toddlers, the toddlers responded by continuing to act on the object, repeating the action with the same object, generating imitation games with the imitator, and looking at the partner's face. Toddlers that were imitated generated longer bouts of joint action and completed more turns in a social bout than toddlers that were interacted with but not imitated (Eckerman & Stein, 1990). Even in older children that have more sophisticated verbal communication skills, imitation remains an important method of conducting social interactions. Abramovitch and Grusec (1978) found that children of four to eleven years of age continue to spontaneously imitate their peers, and that dominant children were more likely to be imitated and also more likely to reciprocate with imitation. In a follow-up study, Grusec and Abramovitch (1982) noted that a child that was playing alone could effectively join a group by imitating one of the members. Another positive consequence of imitation was that imitating generally caused the level

of social interaction already in progress to be either maintained or to increase. Imitators were almost never responded to negatively. The prevalence and context of simultaneous imitation suggests that it is an effective method of social communication.

One reason why imitation may be so effective at facilitating social interactions is that being imitated has reinforcing properties. A common method for assessing the effects of being imitated is to have a subject complete a task that has ambiguous solutions, have one confederate imitate the subject's responses, and another confederate select different responses. Generally, the model subsequently expresses liking the imitator more than the nonimitator, and is more likely to reciprocate by imitating on additional tests. A non-imitative response that is also contingent upon the model's behavior is not shown to have the same effect as imitation, ruling out the possibility that it is predictability that is reinforcing rather than imitation (Fouts, Waldner & Watson, 1976; Smeets & Kauffman, 1983; Thelen, Dollinger, & Roberts, 1975; Thelen & Kirkland, 1976).

The positive effects of imitation may be even more pronounced when the model is overtly attempting to teach a behavior. In one study, female college students taught two seventh-grade male confederates an unusual method for completing a math problem. In a subsequent test in which the students were free to solve math problems by any method they chose, one confederate solved the problems in the manner the teacher had shown them and the other solved the problems with equal accuracy, but using a traditional

method. When the teacher evaluated the students, the imitator was deemed to be more likable, more intelligent, more creative, better adjusted, and more likely to do better in school than the nonimitating student (Roberts, Santogrossi & Thelen, 1980).

Although synchronous imitation is more prevalent in children, the phenomenon is not completely absent in adults, and the behavior appears to retain its positive affect in most circumstances as well as its communicative purpose. A confederate was instructed to imitate subjects' conversational behaviors of posture, vocal pitch, and gross movements of the head, limbs, and trunk. Subsequently, the confederate was rated by most subjects as more competent, socially attractive, and sincere by subjects who were unaware that they had been imitated. If the experimenter casually suggested that the confederate may have been imitating, either intentionally or unintentionally, the subjects' opinions of the confederate became negative (Manusov, 1992). Evidence that imitation retains its communicative purpose is provided by the fact that people will wince to show empathy when another person sustains an injury more often when the injured person makes eye contact than when the person turns away (Bavelas, Black, Lemery & Mullett, 1986).

In summary, synchrony in humans appears to be an important behavior from the time infants are able to achieve synchrony and throughout their lives, although synchrony is most important before verbal language skills are fully developed. Imitation increases

the likability and attractiveness of the imitator, perpetuates social interactions, and generally causes an increase in cohesiveness.

As many species of dolphins are sociable, any behavior that increases the success of social interactions is likely to be valuable to them as well. The outcomes of synchronous and imitative behavior in humans are consistent with things that are desirable in a cetacean community as well – being attractive to conspecifics, prolonged social contact, and cohesiveness between group members.

Synchrony in Dolphins

There have been a few studies that examine cetacean synchrony in general. Dive synchrony has been studied in sperm whales (*Physeter macrocephalus*; Whitehead, 1996) and killer whales (*Orcinus orca*; Bisther & Vongraven, 1995). Synchrony of breathing has been studied in bottlenose dolphins (Mann & Smuts, 1999; Peddemors, 1990) and in killer whales (Ray, et al., 1986). However, there has not previously been a quantitative study of the synchrony of movements of any cetaceans. Even though synchronous behavior is a ubiquitous feature of many species of dolphins' interactions, the nature of the dolphin's aquatic environment makes synchrony an elusive subject of study.

Increased hydrodynamic efficiency has been purported to be a possible function of schooling in cetaceans. Norris and Prescott (1961) reported calves riding the wake of their mothers' pressure waves, an assumption that was supported theoretically by Lang

(1966). Williams, et al. (1992) tested the theory experimentally and found that a bottlenose dolphin was able to swim faster when bow-riding than when free-swimming. Furthermore, the dolphin was able to maintain equal respiration rates and serum lactate concentrations and even lower heart rates while bow-riding. The results indicate that dolphins are able to utilize hydrodynamic disturbances created by larger objects such as boats or whales to their advantage, although the implications for dolphins of equal size swimming together are not known.

A second proposed function of synchrony is that it may enhance predator and prey detection. Norris and Dohl (1980) have speculated that a dolphin school moving in synchrony acts as a single, hyper-sensitive organism, or a *sensory integration system* (SIS). The key to the SIS's heightened abilities is the rapid transmission of information from every individual in the school to every other individual. As long as the members of the pod are in visual contact with each other, subtle deviations in the synchronous movements of one or two members may transmit useful information to the rest of the pod. While some changes in gross movement would be detectable to other dolphins even if the group were swimming in a loose aggregation, the SIS would be more efficient if every member were moving exactly together rather than in a generally similar direction and speed. Subtle changes in movement or eye gaze would not be detectable if the pod were not tuned to a synchronous rhythm or movement pattern. If membership in an SIS

does improve overall vigilance, then synchrony would be beneficial during travelling and foraging.

Detection of predators and prey may also be facilitated by synchrony during periods of passive listening to a neighbor's echolocation click trains. Xitco & Roitblat (1996) demonstrated that a bottlenose dolphin that was prevented from echolocating by positioning his melon above water could nonetheless receive detailed information by listening to another dolphin as he echolocated. The information received was sufficient for the listening dolphin to perform a three-alternative match-to-sample discrimination at 67% accuracy (chance was 33%). In this study, the dolphins were positioned precisely by utilizing a stationing hoop and a bite plate so that the rostrums of the listener and the echolocator were separated by only 30-40 cm, less than 5° relative to the sample object. Although the receptive field of a returning echo encompasses a cone of about 10° (Au & Moore, 1984), it is interesting to note that the listening dolphin often slid along the bite-plate so that he was even closer to the echolocating dolphin than required by the experimenter. In a real-world situation without a stationing apparatus, the best way to maintain this remarkably close spacing for extended periods of time would be to move in synchrony with each other. This also would make synchrony common during travelling and foraging.

A third proposed function of synchrony is that, as with birds and fish, synchrony exhibited within a pod may help protect dolphins from predators via dilution and

confusion effects. Solitary dolphins may be at greater risk of death than dolphins that regularly associate with others simply because within a group, there are more targets to choose from. In addition, moving in unison may contribute to confusion of the predator by causing a visual distraction. The anti-predator advantages of dilution and confusion could help explain why dolphins tend to coalesce into a tightly-formed, highly-synchronous school in response to dangerous or novel situations.

A fourth function of synchrony could be that it is important in social contexts as indicators or reassurances of affiliation, or as a method of maintaining or advertising hierarchical relationships. As an expression of affiliation, moving in synchrony may strengthen mother-calf bonds as well as the bonds among male coalitions. Affiliation expressed in this way may also inform other dolphins that certain individuals have an alliance. That synchrony is often observed during other affiliative acts such as caressing and during bouts of play supports this hypothesis. If it is shown that specific individuals are responsible for maintaining synchrony within a group, then synchrony may also have implications within hierarchical relationships. A dominant animal may routinely enforce synchronous interactions. Alternately, subordinate animals may initiate synchrony as a display of submission or as a method of gaining favor with more powerful members of the group. Similar functions have been attributed to grooming behaviors in primates (Dunbar, 1991).

As a fifth possible function, synchrony may also play a role in imitation as communication or as a learning mechanism. Dolphins are reportedly adept imitators. Tayler and Saayman (1973) observed several occasions of dolphins spontaneously imitating conspecifics and intraspecifics at the Port Elizabeth Oceanarium in Port Elizabeth, South Africa. Haig, a mature bottlenose dolphin female, began to mimic the swimming, resting, and grooming behaviors of a Cape Fur Seal (*Arctocephalus pusillus*) that was housed in the same tank. Haig and other dolphins at the oceanarium were seen imitating a skate (*Raja* sp.), a loggerhead turtle (*Caretta caretta*), a human scuba diver, and a human smoking a cigarette (by using milk in lieu of smoke) with high fidelity. Haig even learned how to use a steel scraper to dislodge and eat seaweed from the tank bottom after watching a diver perform the behavior. Once the scraper was removed, Haig improvised by using a broken ceramic tile to scrape the bottom. Lady Dimple, another female bottlenose dolphin, watched Haig intently and began to imitate this new behavior.

Dolphins have also demonstrated their ability to imitate humans and conspecifics under experimental conditions. In one study involving two bottlenose dolphins, Hiapo and Elele, each dolphin looked on as a human swimmer was given a novel hand signal, performed a novel behavior, and then was rewarded with a fish (which the human put in a pouch). The dolphin was then given the same hand signal to see if it would imitate the new behavior. The same procedure was later repeated using a generic “imitate” hand signal after each demonstration. Both dolphins imitated a significant number of behaviors

under both conditions, in several cases, after the first presentation (Harley, Xitco, Roitblat, & Herman, 1998; Herman, Pack, & Morrel-Samuels, 1993). Other dolphins have performed successfully in similar experiments in which the model was another dolphin instead of a human, and a generic “imitate” signal was used (Bauer & Johnson, 1994; Xitco, Harley, & Brill, 1998).

Interestingly, sometimes the imitator begins imitating before the model finishes modeling so that the behaviors are performed simultaneously (H. Harley, pers. comm.). This suggests that synchrony and imitation may have an intimate connection. Braslau-Schneck (as cited in Connor & Peterson, 1994) reported that two bottlenose dolphins had been trained to perform a unique behavior in response to a “be creative” signal. Each dolphin had also been trained to perform behaviors synchronously in response to a signal. The two signals were then combined into a “creative tandem” command in which the dolphins were required to perform a unique behavior and perform it together. The two responded by circling underwater for awhile before they began to swim synchronously, leapt into the air, and spit water together. Synchrony may itself be a medium of rapid communication between animals that are extremely “in tune” with each other’s most miniscule movements. Synchrony may be the foundation upon which imitation, a sort of delayed synchrony, rests.

An instance of a mother spinner dolphin teaching her calf complex aerial maneuvers (Johnson & Norris, 1994) is another intriguing example of how synchrony

and imitation may work hand in hand to achieve complex goals. The aerial behaviors of young spinner dolphins are often uncoordinated and imprecise; learning and practice is required before the juvenile's leaps and spins attain the smooth coordination of adult leaps. Oftentimes, parents and alloparents are seen performing aerial maneuvers with young calves, which Johnson and Norris have speculated may be an example of teaching. In one instance, a mother and her calf were seen leaping in synchrony for up to 13 leaps in a row. If the mother were providing an opportunity for the calf to practice its skills by leaping more often when the pair was swimming synchronously, or if she was enforcing synchronous swimming while leaping, it could be considered teaching (Caro & Hauser, 1992). In a variety of circumstances, synchronous behavior could be an efficient manner in which to teach a calf new skills.

In summary, synchrony has been observed in several contexts: while travelling, foraging and feeding, in response to stressful situations, while playing, possibly while teaching, and during affiliative and sexual behaviors. Travelling and foraging in synchrony may be related to energy conservation, increased awareness of predators and prey as a sensory integration system, and predator avoidance through dilution and confusion effects. Synchronous reactions to novel or threatening situations may be a generalized anti-predator response. Synchrony may be a medium of communication while playing and teaching, and also may be a display of affiliation and/or hierarchical

status to partners and other pod members. Of course, it is likely that synchrony plays more than one role in each these contexts.

Mother-Calf Dolphin Behavior

Several observations of early mother-calf behavior have been reported for bottlenose dolphins (Dudok van Heel & Meyer, 1974; Johnson & Norris, 1994; McBride & Hebb, 1948; McBride & Kritzler, 1951; Tavalga, 1966; Tavalga & Essapian, 1957; Wells, 1991). Gestation is known to be approximately 12 months (Harrison, 1969); labor can be as short as 20 minutes or as long as several hours. During labor, the mother will often remain at the surface and flex her peduncle up and down as if stretching. The calf is delivered in a breech presentation, with the flukes advancing and retreating several times before the calf is finally released. Immediately after birth, the umbilical cord breaks, and the calf swims to the surface for its first breath. Occasionally, the mother or another dolphin aids it to the surface by pushing it upwards. Although the dorsal fin and flukes are infirm or floppy for several hours, the calf is precocial and is capable of swimming immediately. Infants are born with or quickly develop a strong tendency to follow. Very young calves that have been temporarily separated from their mothers have reportedly followed other tankmates, even males (McBride & Kritzler, 1951). Often, an alloparent or “auntie” will accompany the calf until the mother passes the placenta or while the

mother is foraging or feeding. Otherwise, the calf stays with the mother nearly all of the time.

Suckling behavior is generally observed within two to six hours after birth (Dudok van Heel & Meyer, 1974; Reid, Mann, Weiner, & Hecker, 1995; Schroeder, 1990; Triossi, Pace, Terranova, & Renzi, 1998), although Eastcott and Dickinson (1987) report one notable exception where the calf did not even attempt to suckle until she was 17 hours of age and was not successful until she was 21 hours old. Suckling occurs most often during the first week of the calf's life and gradually decreases in frequency until weaning. Throughout the first year, bouts of suckling occur on average two to four times per hour (Cockcroft & Ross, 1990; Dudok van Heel & Meyer, 1974; Eastcott & Dickinson, 1987; Peddemors, Fothergill, & Cockcroft, 1992; Reid, et al., 1995; Schroeder, 1990), and each suckle lasts three to ten seconds (Cockcroft & Ross, 1990; Eastcott & Dickinson, 1987; Mann & Smuts, 1999; Peddemors, et al., 1992; Reid, et al., 1995; Triossi, et al., 1998).

Every calf that is to survive requires the constant, unwavering attention of its mother or an alloparent. In most cases, the calf remains at the mother's side almost exclusively. The mother is capable of directing the calf's behavior in this position by herding it away from walls, dangerous objects, predators, and other dolphins (Cockcroft & Ross, 1990). In captivity, the mother will often create a "playpen" by continually circumnavigating the perimeter of the tank, keeping the calf on the inside of this circular

path (Bateson, 1974). In the first days of life, any attempt by the calf to stray from the mother's side is met with immediate retrieval and sometimes punishment. Punishment takes the form of being held to the bottom for up to a minute, or being immobilized above the surface of the water on the mother's belly for several seconds (Dudok van Heel & Meyer, 1974; Tavalga, 1966; Tavalga & Essapian, 1957). In the wild, maternal groups often travel with one or more calves swimming between two or more adult females, forming a second type of "playpen" (Bel'kovitch, 1991). Failure of the mother or alloparent to strictly control the calf's movements generally leads directly to the calf's death (Dudok van Heel & Meyer, 1974; Johnson & Norris, 1994; Tavalga & Essapian, 1957).

During the first one to two months, the mother and infant are found most often with the calf swimming next to the mother's dorsal fin, and the pair are either in direct contact or very near each other (Echelon position). Respiration during this time is highly synchronous (Mann & Smuts, 1999; Peddemors, 1990). It is thought that the calf receives a hydrodynamic advantage by maintaining this position in that it is carried along in the pressure wave created by its mother (Norris & Prescott, 1961). The calf is able to keep up with its mother, even at top speed, and the calf's tail generally does not beat at the high rate that would be expected during high-speed travel (Wells, 1991). After the first one to two months, the calf then shifts to maintaining a more caudal position under the mother's tail (Infant position; Cockcroft & Ross, 1990; Connor, Wells, Mann, & Read, 2000;

Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999) and can be seen swimming regularly with other companions (Tavolga & Essapian, 1957). By this time, it has presumably attained the skills that allow it to leave the mother's slipstream.

The transition of the calf from swimming primarily in Echelon position to Infant position marks the beginning of its gradual shift towards independence. Although the association remains strong between mother and calf for three years or more, the calf begins swimming away from its mother increasingly often and for longer periods of time (Cockcroft & Ross, 1990; Connor, et al., 2000; Gubbins, et al., 1999; Mann & Smuts, 1999). The calf begins to take a few fish sometime between six and twelve months of age, but continues to nurse in decreasing amounts until as old as four years (Peddemors, et al., 1992; Wells, 1991). The calf and mother continue to maintain strong bonds throughout weaning, and the calf will return to swim with its mother when threatened or tired (Essapian, 1953).

Since behavioral synchrony has not been studied previously, investigating the synchrony of a mother-calf pair seems like a natural place to start. Although synchrony appears to be present in many cetacean relationships, nowhere is it more prevalent than between a mother and her young calf. Specific characteristics of synchrony are likely to be expressed differently between mother and calf than between adults, and it is hoped that some of the important differences will become apparent during these observations. The primary goals of this study are to 1) determine when synchronous behavior first

appears, 2) measure how prevalent synchrony is during the first month of a calf's life, 3) quantify specific characteristics of synchrony such as frequency and spatial relationships, 4) observe any trends that may occur over the course of the observation period, and 5) speculate on possible functions of synchrony.

Method

Participants

Naia, a captive-born female bottlenose dolphin (*Tursiops truncatus*), was the focal animal in this study during the first four weeks of her life. Naia's tankmate throughout the study was her mother, Noriko, an adult bottlenose dolphin. Naia was Noriko's first calf and has survived to six years of age at the time of this writing. Noriko and Naia were housed at The Living Seas at Disney's EPCOT in Orlando, Florida. At the time of observation, they remained in a 20-ft by 25 ft by 6-ft rectangular research pool that was adjoined via a flow-through gate to another pool of similar measurements. The gate was closed for the first week after Naia's birth, but was open for the remainder of the study. Although the pair was free to move between both tanks, they were never observed to do so during the study period. A 6.5 million-gallon, 27-ft deep viewing tank was connected to the research pools, but the dolphins' access was restricted to the research pools during the early stages of Naia's infancy for safety reasons.

Two other adult female bottlenose dolphins shared living quarters with Noriko before and after Naia's birth, with the exception of Naia's first week. Nina was Noriko's most frequent companion, and Snapper was more likely to swim alone. Neither Nina nor Snapper were presumed to have previously given birth, though their detailed histories were not available to the experimenter. Two adult male bottlenose dolphins inhabited the large viewing tank throughout the study, but were not in contact with any of the animals under observation.

Materials

A black and white video camera (Sony SSC-M370 B/W CCD) and VCR (Sony SVP-120) recorded the movements of Naia and Noriko at regularly programmed intervals. The camera was mounted directly above the center of the research pool, and its view encompassed the entire area that the mother and calf could access within that pool. A date/timestamp recorded the time to the nearest second in the upper right corner of the video. The timestamp partially obscured approximately 5.5% of the view.

Procedure

Recording began at 0200, less than one hour after Naia's birth. Noriko and Naia were recorded continuously for 12 hours, and the first five minutes of every hour were analyzed. At 1800, the video camera began recording the initial five minutes every two-hour period. On the 7th day, the two other adult female bottlenose dolphins were

reintroduced to Noriko and Naia's tank. At times, the other adults swam into the other pool, but their access to the mother-calf pair was never restricted after the first week.

A focal-animal sampling technique (Altmann, 1974) was used in which 117 5-minute video segments were analyzed for mother-calf synchrony. The samples were distributed over the four-week observation period with a majority of the observations occurring during the first week when changes in the calf's behavior were occurring rapidly. Thirty-seven segments were then analyzed a second and third time with the calf and the other two females as the focal pairs. This procedure yielded a total of 400 minutes of observations while the mother and calf were alone, and 185 minutes while all four dolphins were together that was analyzed three times – once for each focal pair (Table 1). In addition, pilot data were collected on Noriko with each of her two female tankmates one month (6 segments) and one week (7 segments) prior to Naia's birth.

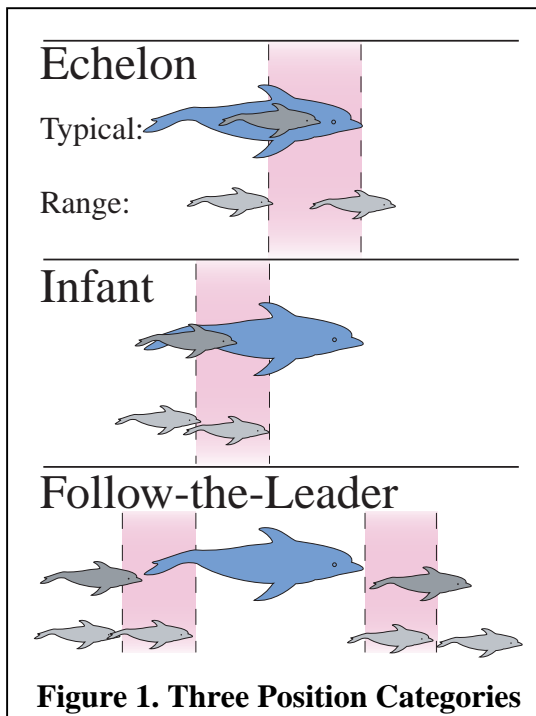
Community State:	Alone	All four dolphins together		
	Mother-Calf	Mother-Calf	Calf-Nina	Calf-Snapper
Week 1	80 seg/400 min	n/a	n/a	n/a
Week 2	n/a	19 seg/95 min	19 seg/95 min	19 seg/95 min
Week 3	n/a	12 seg/60 min	12 seg/60 min	12 seg/60 min
Week 4	n/a	6 seg/30 min	6 seg/30 min	6 seg/30 min
Total	80 seg/400 min	37 seg/185 min	37 seg/185 min	37 seg/185 min

Table 1. Total Number of Segments/Minutes Analyzed.

Each segment was microanalyzed continuously, second-by-second for synchronous behavior. When both members of the focal pair were moving synchronously, specific characteristics of body position and proximity were recorded (see Appendix A for an example of the data collected during a typical segment).

Synchrony. Synchrony was defined as being engaged in the same swimming state (i.e., swimming, floating, or spyhopping) while the dolphin's bodies were within 10° of being parallel. If one dolphin was required to turn before the other during a bout of synchrony to avoid connecting with a wall, it was not considered a break as long as synchrony was resumed within 1 second. Several changes in position and proximity could take place within a single bout of synchrony, which was called a "variable bout" because the individual characteristics could vary. Each variable bout of synchrony could in turn be composed of one or more "static bouts" of synchrony. In a static bout, absolutely no changes occurred from beginning to end. In other words, if the calf was in infant position for 10 seconds, moved to echelon position for 20 seconds, returned to infant position for 5 seconds, then broke off, the details of three static bouts of synchrony and one 35-second variable bout were recorded. Variable bouts were always separated by breaks in synchrony.

Position. Body position was divided into three categories: Echelon, Infant, and Follow-the-Leader. When the dolphins were in echelon position, they were next to each



other, with one dolphin's rostrum no further back than the trailing edge of the leading dolphin's dorsal fin. In the infant position, one dolphin's rostrum was within the area of the partner's mammary slits: behind the other's dorsal fin and in front of the base of the other dolphin's flukes. It was possible for the mother or other adults to be in the infant position.

While in the follow-the-leader position, one dolphin was in front of the other, with the follower at least behind the base of the leading dolphin's flukes (Figure 1).

Proximity. Proximity was divided into four categories: Touching, near, intermediate, and far. Touching was direct physical contact by fins or other body parts and could occur in any position. While touching, the specific body parts in contact with each other were noted. The dolphins were recorded as being near each other when each was within a maximum of one adult body width. The dolphins' proximity was far if each dolphin was within one body width of opposite walls of the tank, as far away from each other as possible within their enclosure. Intermediate proximity was any distance that was between near and far.

Suckling. Suckling was recorded when the calf was in the infant position, her rostrum appeared to be in direct contact with Noriko's mammary area, and she was

locked on. Possible suckling was recorded when Naia was in the correct body position, but because of camera angle or unusual behavior, it wasn't possible to be certain that the calf was actually suckling. All other circumstances were recorded as not suckling.

Initiator/Terminator. When one dolphin changed its swim state and/or orientation to match that of another dolphin, it was said to have initiated synchrony even though it appeared to be the second animal to begin performing the behavior. The first dolphin to break away from the other was the one that terminated synchrony. Simultaneous changes were recorded as "both". If it was not possible to see the dolphins when a bout of synchrony began or ended because they were under the timestamp or a reflected glare on the surface of the water, these situations were recorded as "obscured". A crossover occurred when the dolphins were moving synchronously, crossed over or under the other, and then continued to maintain synchrony. Crossovers often occurred several times within one bout of synchrony and were noted only for number of occurrences. A break was not recorded when the calf drifted to an angle greater than 10° while suckling, but was still clearly attached to the mother, or during crossovers.

Path. During the first week, characteristics of the swimming paths of mother and calf were also categorized for the entirety of each time segment, whether they were synchronous or not. Specifically, it was recorded whether they swam clockwise, counter-clockwise, or in neither direction, and whether the calf swam on the inside or outside of the mother's circular path, or was swimming independently.

A second person analyzed six randomly-chosen segments in exactly the same manner as described above as a verification of coder reliability. The results were then compared second-by-second to assess agreement between the two coders. A total of 1800 seconds were compared. Overall reliability was high (.91) with results ranging from .82 (which body parts were touching) to 1.00 (swim state). Most discrepancies involved disagreements of exactly when a transition occurred.

RESULTS

Overall Synchrony

Synchrony was maintained 97.7% of the time and was a dominating characteristic of early mother-calf interactions. The proportion changed very little throughout the study. There was an average of 1.0 breaks in synchrony per 5-minute sample with each break lasting an average of 7 s (SD = 5 s). Static bouts of synchrony lasted 13 s on average (SD = 23 s), and variable bouts lasted 2 min 31 s (SD = 2 min 1 s). Suckling was first observed 16 h after birth, and each bout lasted an average of 8 s (SD = 1 s).

The mother initiated most bouts of synchrony (74.3%), although there were several instances where both dolphins changed their behavior to come together simultaneously (14.9%). The calf terminated more bouts than the mother (57.5% vs. 33.6%) and only 5.3% were jointly terminated. The initiating or terminating dolphin was

unknown in 2.0% of the initiations and 3.5% of the terminations because they were concealed behind the timestamp or a glare on the water.

Hinde's Index of Association (Hinde & Atkinson, 1970) was used to determine which partner was primarily responsible for maintaining synchrony. Hinde's Index (HI) states that $HI = [U_m / (U_m + U_c)] - [S_m / (S_m + S_c)]$, where U represents Unifications, S represents Separations, and the subscripts m and c represent the mother and the calf, respectively. The HI can range from +1 (mother completely responsible) to -1 (calf completely responsible). An HI of 0 indicates that responsibility for maintaining synchrony is shared equally between partners. Only instances in which one partner or the other was clearly responsible for a unification or separation were considered; cases in which both changed their behavior simultaneously were not included in the calculation. Noriko and Naia's HI was +0.5, indicating that responsibility for synchrony fell primarily on the mother.

While swimming synchronously, the calf spent the majority of her time in Echelon position (90.1%), followed by Infant position (6.8%), Mom in Calf Position (2.0%), Calf Leading Mom (1.0%), then Mom Leading Calf (0.01%). Naia spent most of her time in Touching proximity (82.3%), followed by Near (17.1%), then Intermediate (0.5%). There were no instances of Far proximity. When the pair was swimming synchronously while touching, the body parts most frequently in contact with each other were calf's trunk to mother's trunk (80.8%), calf's pectoral flipper to mother's trunk

(8.9%), calf's rostrum to mother's trunk which generally represented suckling (7.7%), mother's pectoral flipper to calf's trunk (1.6%), and mother's rostrum to calf's trunk (1.0%).

Developmental Changes

Several changes were observed at the commencement of suckling. Suckling was first observed 16 hours after Naia's birth. The first week of the observational period was divided into three phases with respect to the onset of suckling. The Pre-Suckling phase spanned Hours 1 through 15, Early Suckling was used to describe the 24-hour period after suckling was first observed (Hours 16 through 40), and the Established Suckling phase included all observations after Hour 40 through the end of the week. The Pre-Suckling phase was characterized by a small amount of asynchrony, almost no occurrences of the calf swimming outside of the mother's circular path, little swimming in a clockwise direction, and no more than six crossovers per 5-minute sample ($M = 1.3$). The Early Suckling phase was characterized by a peak in asynchrony, the calf swimming outside the path quite often, much more clockwise swimming, and a maximum of only one crossover per sample ($M = 0.6$). In the Established Suckling phase, asynchrony nearly disappeared, the calf swam slightly less often on the outside, clockwise swimming dropped dramatically, and a maximum of 13 crossovers were seen per 5-minute sample ($M = 2.8$). The general patterns of synchronous behavior instituted in the Suckling Established phase changed little during the following three weeks (Figures 2, 3 and 4).

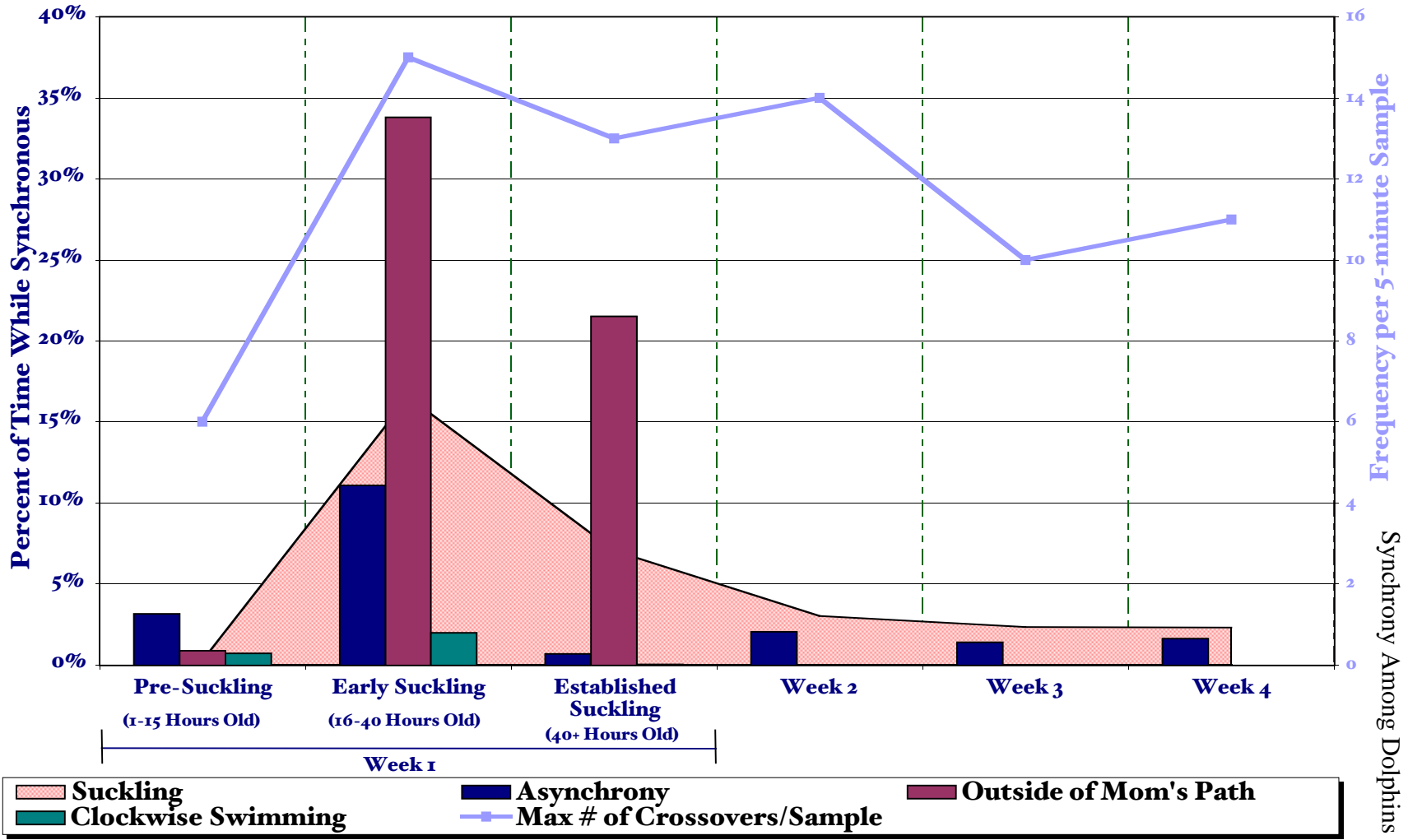


Figure 2. Effects Co-Occurring with the Onset of Suckling. The period in which the calf first began to suckle was associated with a brief period of disorganization, indicated by an increase in asynchrony and travelling clockwise, counter to the mother's preferred direction. As suckling became established, the number of crossovers increased, and the calf was then allowed to swim either the inside or the outside of the mother's circular path. (Note that data for the path characteristics of clockwise swimming and swimming outside are only provided for the first week).

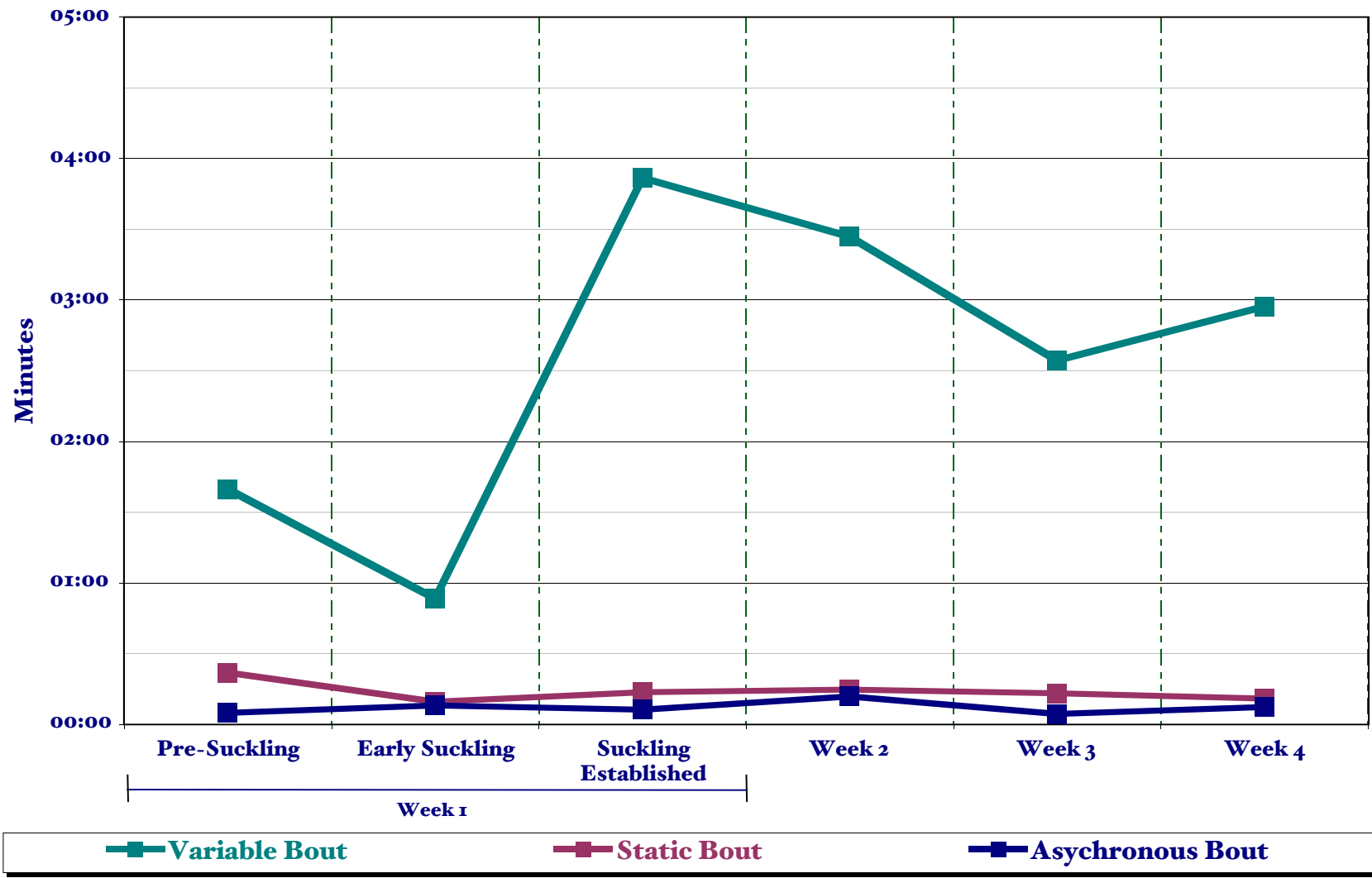


Figure 3. Average Length of Bouts per 5-Minute Sample. Variable bouts of synchrony increased after the calf began suckling even though the length of static bouts remained constant. There was also no change in the length of asynchronous bouts.

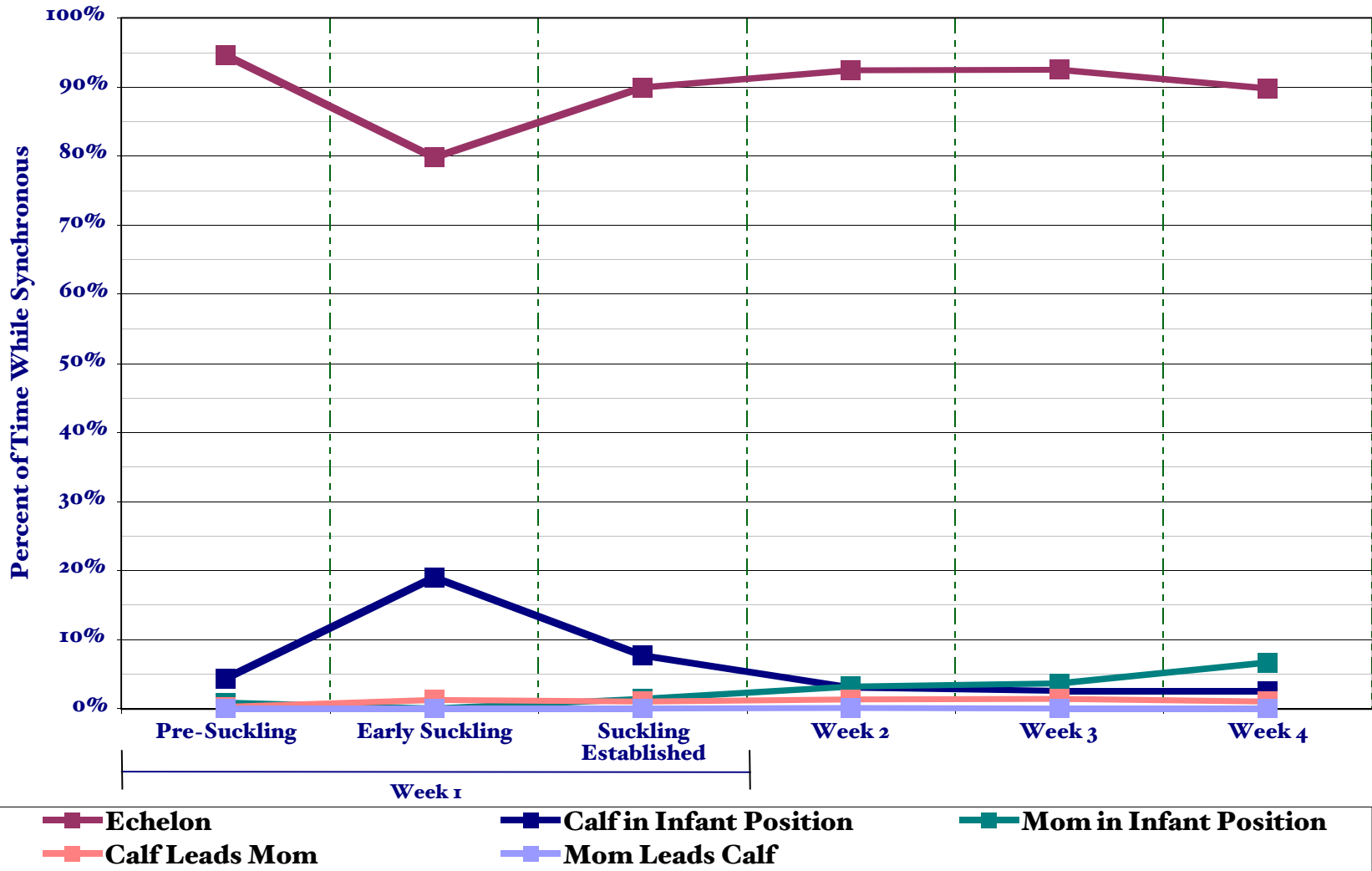


Figure 4. Percent of Time Spent Synchronously with the Mother in Each Position. The calf swam in echelon position most frequently. An increase in Calf in Infant position occurred at the onset of suckling and then subsided. There was a slight positive trend by the fourth week for the mother to swim in Infant position, indicating that she was beginning to allow the calf to swim slightly ahead of her.

Although many characteristics of synchrony remained relatively stable after suckling was established, one property that changed was responsibility for maintaining synchrony. The calf only initiated a single bout of synchrony during the first two weeks. In the third and fourth weeks, however, the calf initiated 50.0% of the bouts. The mother initiated 75% or more of the bouts during the first two weeks, but only 41.7% during Week 3 and none during Week 4. Both dolphins came together simultaneously only about 15% of the time initially, but did so 50.0% of the time by Week 4. The HI fell from 0.5 to 0.0 accordingly, indicating that in the fourth week, responsibility for maintaining synchrony was shared (see Table 2), although it should be remembered that the “Both” category was not considered when figuring Hinde’s Index.

	Mother	Calf	Both	Obscured	Hinde’s Index
Pre-Suckling	81.0%/50.0%	0.0%/50.0%	14.3%/0.0%	4.8%/0.0%	+ 0.5
Early Suckling	81.6%/41.7%	2.6%/47.9%	15.8%/6.3%	0.0%/4.2%	+ 0.5
Established Suckling	77.8%/35.3%	0.0%/41.2%	16.7%/11.8%	5.6%/11.8%	+ 0.5
Week 2	100.0%/0.0%	0.0%/88.9%	0.0%/11.1%	0.0%/0.0%	+ 1.0
Week 3	41.7%/0.0%	50.0%/100.0%	8.3%/0.0%	0.0%/0.0%	+ 0.5
Week 4	0.0%/0.0%	50.0%/100.0%	50.0%/0.0%	0.0%/0.0%	+ 0.0
Overall	74.3%/33.6%	8.9%/57.5%	14.9%/5.3%	2.0%/3.5%	+ 0.5

Table 2. Percentage of Bouts Initiated/Terminated by Each Partner.

Another characteristic that changed was the proximity maintained between the mother and calf. In the hours after birth and before suckling was initiated, the calf spent 94.1% of her time in direct contact with her mother. The amount of time spent touching dropped substantially to 66.0% during the Early Suckling phase but rebounded to 84.8% after suckling was well established. The amount of time spent touching then gradually declined through Week 4. As time spent touching decreased, the amount of time spent in the Near position increased (Figure 5).

Calf's Behavior with Other Adult Females

The two other adult females periodically swam with the mother-calf pair. Although the recorded characteristics of proximity and position pertained specifically to the calf's relationship to the other adults, it is important to note that the mother was always present in each interaction.

The calf was synchronous more often with Nina (54.7%) than with Snapper (8.7%). The calf was rarely in direct contact with either of the other adults (<1%). The most frequent proximity with both Nina and Snapper was Near (59.0% and 62.1%, respectively), but Intermediate comprised a substantial minority (40.1% and 37.7%, respectively). In relation to Nina, the calf was most commonly found in Echelon position (66.6%), followed by Calf in Infant position (12.8%), Calf Leading Nina (10.4%), Nina Leading Calf (6.3%), and Nina in Infant position (3.9%). Echelon position was also

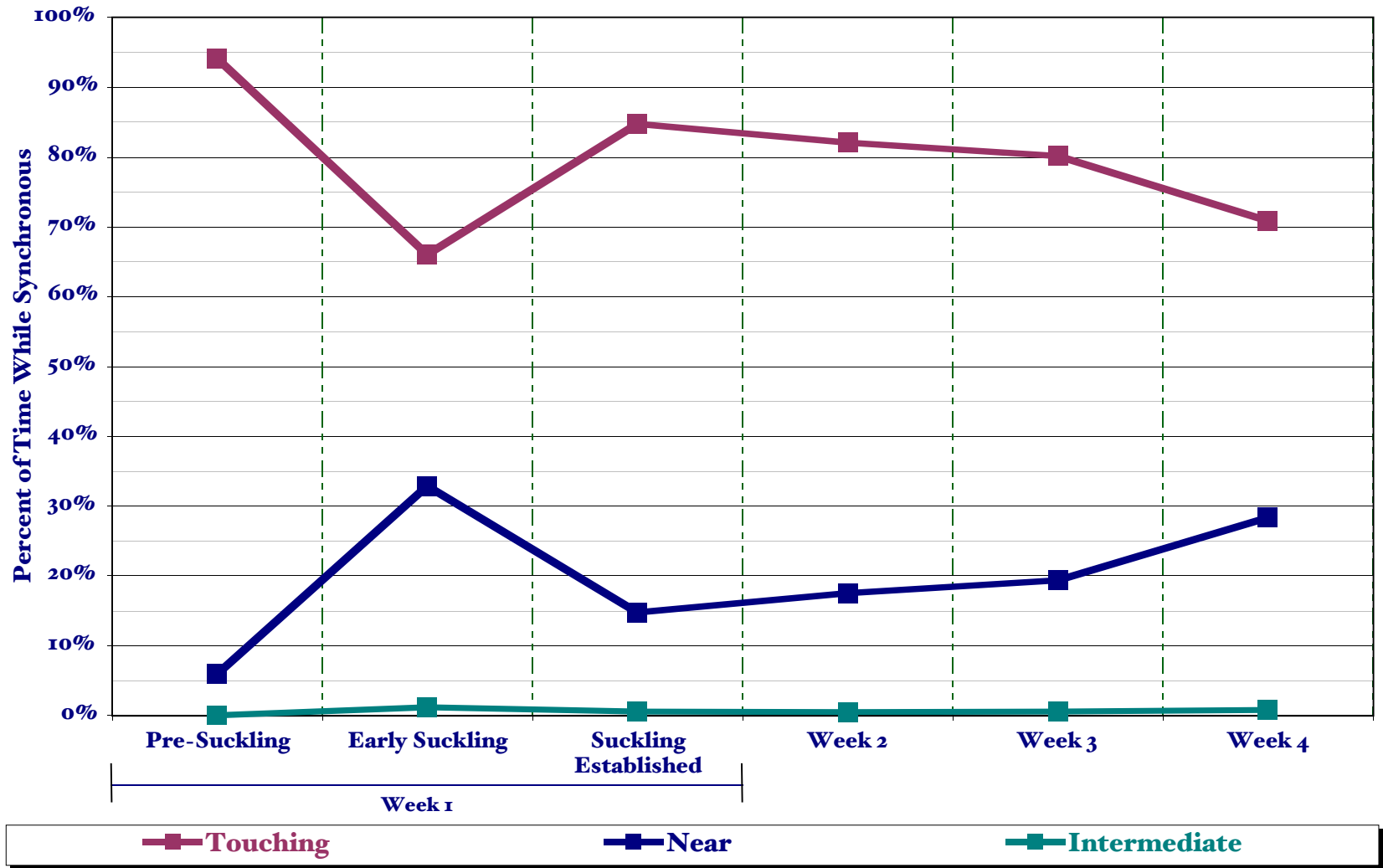


Figure 5. Percent of Time Spent Synchronously with the Mother at Each Proximity. The calf spent the majority of her time in direct contact with her mother. While suckling behavior was becoming established, there was an increase in the calf swimming at Near proximity to her mother. Although Touching was still the most frequently-observed proximity, there was a trend for the calf to be Near more often and Touching less often.

the most frequent position with Snapper (66.4%), followed by Snapper in Infant position (15.7%), Calf Leading Snapper (13.1%), Calf in Infant position (2.6%), and Snapper Leading Calf (1.4%). These proportions remained relatively stable throughout the observation period (Figure 6).

DISCUSSION

Development of Synchrony

Synchrony is clearly an important component in early mother-calf interaction, as there was not a single activity other than swimming in general that was observed more often than moving in unison. Particularly interesting was the finding that dramatic changes in synchrony occurred during the onset of suckling behavior. During the Pre-Suckling phase in the first week, the mother appeared to be almost entirely in charge of her calf. The calf was nearly always kept to the inside of the mother's circular path, with her trunk nearly always in direct contact with her mother's trunk. Most observed interactions appeared calm and stereotyped, and proceeded almost exclusively in the mother's preferred direction of counter-clockwise. In fact, there were two completely synchronous 5-minute observations in which the pair travelled trunk-to-trunk in a counter-clockwise direction with the calf on the inside for the entire observation period: one at two hours and the other at three hours after birth. At ten hours after birth, another session occurred that was also stereotypical for all but five seconds of the interaction. In

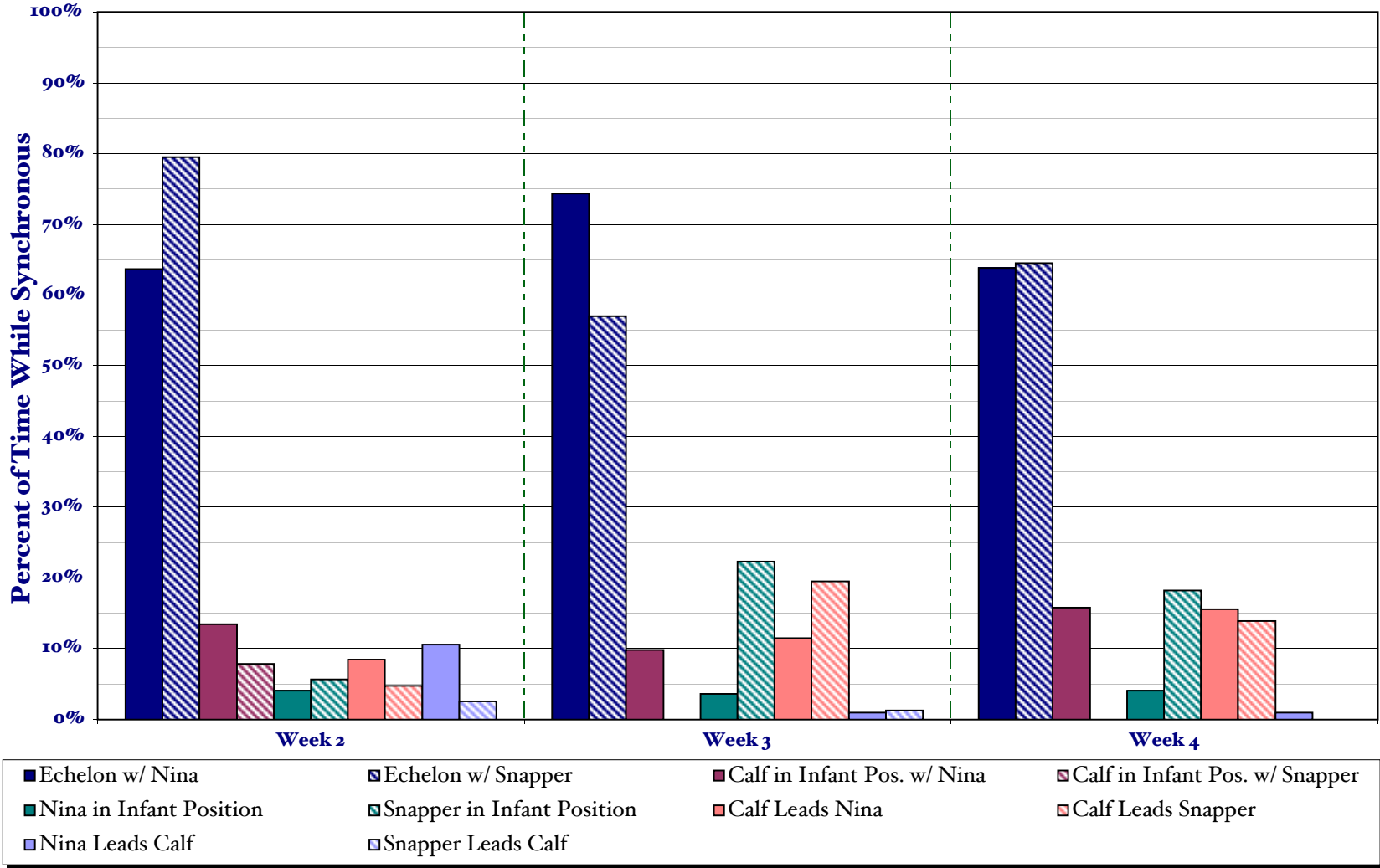


Figure 6. Changes in Positions while Synchronous with Nina and Snapper. Echelon swimming was most common with both of the other adult females. Note that from Week 3 on, Nina preferred to be slightly ahead of the calf while Snapper preferred to be slightly behind. In fact, the calf was never in Infant position with Snapper after Week 2. Nina is represented by the solid bars, Snapper by the striped bars.

other sessions during this phase, if the calf managed to break away briefly (5 s on average) from the mother, she was able to react quickly to regain control of her calf and in order to prevent her from running into a wall. The high amount of touching observed suggests that the mother could be “steering” her calf around the tank. Alternatively, the calf could be riding her mother’s slipstream. The calf’s ability to stay with her mother immediately after birth, even at high speeds, suggests that she was being helped along in some manner, either through direct physical support or via slipstreaming.

The onset of prolonged suckling behavior was first observed at 1800 hrs, approximately 16 hours after the calf’s birth. Within two hours of beginning to suckle, the calf was observed negotiating corners successfully while at a distance from her mother. Four hours after that, the calf began to swim on the outside of her mother’s path, a behavior that comprised 62% of that session, a remarkable difference from the 1% or less observed previously. The number of crossovers also increased commensurately. Also during that session, the mother ceased swimming for 19 s and floated in place; the calf responded by swimming in a tight circle around her three times until her mother resumed their normal course around the circumference of the tank. The pair repeated this circling behavior a second and third time two and four hours later.

With the increased amount of freedom, however, came a risk for the calf of swimming into the walls of the tank or being struck by other dolphins. The Early Suckling phase was represented by the highest degree of asynchrony (11.1%) of any

other time period, a proportion that nearly quadrupled from the previous phase (3.2%). The reason for the increased asynchrony could be attributed to maternal fatigue, or it could be the result of the mother waiting to observe the calf's behavior before reacting to it. Even a moment's hesitation could provide sufficient time for the calf to behave unpredictably. Whatever the cause of the increase in asynchrony, the result was several harrowing moments in which the mother only succeeded in intervening between her calf and a wall at the last instant before a collision. A last-second intervention often necessitated a reversal of direction so that the pair wound up swimming clockwise with the calf recaptured inside the path once again.

Twenty-four hours after the onset of suckling behavior, the overall picture of synchrony had changed once again. Once the suckling behavior was firmly established, asynchrony nearly disappeared, accounting for only 0.7% of the calf's time. The majority of interactions appeared very calm and orderly, and the calf was still able to move freely back and forth between the inside and outside of the path. Interestingly, although static bouts of synchrony did not change appreciably throughout the study, the length of a variable bout increased by over 400%, rising from an average of only 53 s in the Early Suckling phase to 3 min 52 s in the Suckling Established phase. Note that this is out of a possible maximum of only 5 minutes, the length of the sampling period. This pattern indicates that although specific parameters of synchrony such as position or proximity aren't changing any less frequently, those changes are less likely to cause a

break in synchrony because one or both partners is able to compensate and smoothly match the changes.

The question becomes what caused the sudden changes observed between the mother and her calf? One possibility is that the calf had simply developed biologically to the point where she could control some aspects of synchrony. If this were the case, we should expect that in observations of other calves, a similar timetable would be followed. An alternate possibility is that nursing, i.e., milk, acted as a reinforcer for staying close to the mother and that the calf learned how to maintain synchrony by being reinforced for it. It is interesting that so many changes happened so suddenly once suckling began, but it is impossible to know whether it was biological maturation or learning that was responsible for those changes after observing only a single mother-calf pair. The fact that nursing first occurred relatively late (16 hrs vs. 2-6 hrs in most other accounts) lends support for the learning hypothesis.

Once a calm pattern of interaction was established, it continued throughout the fourth week, and levels of asynchrony remained low. The mother allowed the calf to make a single brief foray away from her, which lasted 20 s, for the first time during the Early Suckling phase. Another single foray lasting 7 s occurred during the Established Suckling phase. During the second week, however, the calf began swimming independently more often. Most of her earliest attempts to swim away appeared uncoordinated and “wobbly,” much like a newborn ungulate or a new bicyclist whose

training wheels have just been removed. The calf's forward motion often vacillated somewhat left to right, and most turns were very wide. Also during the second week, the mother began swimming in Infant position more often than in the previous week. It often appeared that she was hanging back to let the calf lead. Synchrony was maintained in these cases, but it may have been the case that the mother was synchronizing her actions to those of the exploring calf. This was a trend that increased through the fourth week.

The calf's preference for remaining in Echelon position is consistent with other accounts of early mother-calf behaviors. However, she had not made the transition to Infant position by the fourth week and was still exhibiting the high degree of synchrony normally characteristic of younger calves. This may be a reflection of maternal inexperience, the mother having a particularly restrictive maternal style, slow development by the calf, or a lack of pressure to achieve independence quickly as the result of being in a captive environment.

Possible Functions

Synchronous swimming in cetaceans is likely to provide many of the same advantages as does schooling in fish and flocking in birds. The advantages of schooling and flocking are thought to be hydro- or aerodynamic energy conservation, increased vigilance for predators and prey, and decreased predation because of dilution or confusion effects.

Most studies or observations of hydrodynamics in cetaceans have involved subjects of unequal size, e.g., adult dolphins bow-riding with boats (Williams, et al., 1992) or large whales, or calves slipstreaming with their mothers (Norris & Prescott, 1961). The fact that the calf appeared to be swimming strongly right after birth but then swam much more uncertainly when swimming independently two weeks later suggests that the calf was utilizing her mother's slipstream to aid locomotion.

Increased vigilance is at the heart of the sensory integration system (SIS) proposed by Norris and Dohl (1980) and Norris and Johnson (1994). The mother's ability to maintain synchrony while in Infant position may mean that, as an adult, she is skilled at causing her movements to match those of another in order to maintain the unified movements of the pod. Examination of reaction times of synchronous pairs could reveal whether their adjustments to each other are quicker than predicted by normal reaction times. Quicker reaction times would indicate a higher degree of attunement to the movement patterns of others, which would allow greater accuracy in judging what the next move might be, just as in the human waltzers discussed earlier.

Synchronous movements could also decrease a predator's chances of executing a successful attack. As mentioned previously, many authors have reported that groups of dolphins will become more synchronous when threatened by novel or dangerous situations. That observation was confirmed in this study. Whenever the mother became agitated, she swam very rapidly and the pair returned to their earlier pattern of

maintaining Touching proximity with trunk-to-trunk contact. In one session observed during the Established Suckling phase, someone started using a skimmer to scoop something from the tank during the last minute of the sample. Although the pair had exhibited the normal amount of variation in position and proximity during the first four minutes of the sample (24 static bouts were recorded), the last minute was subsumed entirely by a single static bout in Echelon position, Touching trunk-to-trunk. The increase in speed may help corral the calf into the mother's slipstream, enabling the pair to look more like a single, large animal to predators (Cockcroft & Ross, 1990).

The most interesting function of synchrony may be as a possible communication tool. In humans, social coordination is generally high when the bonds between parents and children are strong, and imitation is associated with increased likability and prolonged social interactions. For young children who have yet to develop sophisticated language skills, imitation may be a primary means of communicating with playmates or other social partners. Likewise, synchrony could be an efficient manner in which to strengthen bonds, establish social relationships, and mediate social interactions for dolphins as well. Being in a state of synchrony is one of a newborn calf's first experiences. Over time, synchrony within the mother-calf relationship is likely to become associated with safety and being nurtured, and also with having a strong bond. With such precedence, synchrony in future relationships may assume similar meanings. Initiation of

synchrony may signify affiliation or a desire to establish an affiliative relationship.

Maintaining synchrony may also be reassuring in times of stress.

Future Research

Replications of this study are necessary to be certain that the observations reported here are representative of the species and not peculiar to these individuals. However, the consistencies in the mother-infant positions and nursing characteristics observed between this study and previous reports suggest that Noriko and Naia's behavior is typical. It would be especially interesting to know whether the dramatic changes in synchrony that occurred from 16 to 40 hours after birth are associated with the onset of nursing or are merely developmental changes that normally occur during that time period. Future studies that focus on the first two or three days of life could easily investigate that question.

Observations at later time periods could identify at what point the mother and calf begin to behave like other adult pairs and could also be used to examine the relationships between daughters and even granddaughters. Multiple generations of females have been known to associate with each other as adults in the well-studied Sarasota population of bottlenose dolphins (Wells, 1991). Having a measure of synchrony could provide a more robust picture of their relationships over and above the association index.

Although synchrony is generally ubiquitous, the overall amount of synchrony was observed to vary between different partners. Measures of synchrony could be used to

investigate other relationships within cetacean communities. The pilot data from the adults collected prior to the calf's birth suggested that characteristics of adult relationships between females change during pregnancy, particularly when parturition is imminent. The relationship between male dyads could also be investigated. After the mother-calf bond, the male-male bond is purported to be the strongest of all relationships among bottlenose dolphins (Wells, Irvine, & Scott, 1980). It would be interesting to compare the characteristics of synchrony between these two distinct but important relationships.

Since synchronous relationships are differential between individual pairs, it is possible that hierarchical relationships will be reflected in synchronous behavior. Cetaceans in captivity have been shown to exist in hierarchies (Bateson, 1974), and hierarchical relationships are also likely to be present in free-ranging populations (Wells, et al., 1980). Measures of synchrony could be used to see if there is a relationship between status and responsibility for maintenance of synchrony. High status members may choose which individuals to be synchronous with and therefore be more responsible for synchrony. Alternatively, low status members may maintain synchrony as a way of ingratiating themselves with higher status individuals. If such a correlation could be found in a captive population, the knowledge might be applicable to observations of wild populations in which monitoring of complex, lengthy behavior patterns is difficult.

On a practical note, future studies could investigate whether there is a relationship between levels of synchrony and whether a new member will be accepted into an established captive group. There is some risk involved in introducing any new individual to a group as the newcomer may be rejected and become the object of aggression. Any early indicators of group acceptance or rejection before overt aggression becomes obvious would be useful in protecting the safety of each individual.

Finally, synchrony may be useful as a measure of health. Cetaceans often mask signs of illness until they are seriously ill, so the early detection of illness is valuable. Since cetaceans are known for supporting gravely ill group members (Caldwell & Caldwell, 1966), it may be true that earlier signs of support, though subtle, could indicate an impending health threat. In this case, a sudden increase in synchrony may indicate that one member is becoming fatigued and is conserving energy by slipstreaming with other group members. Conversely, a sudden decrease in synchrony could indicate that an individual is having difficulty maintaining normal social patterns.

References

- Abrahams, M.V., & Colgan, P.W. (1985). Risk of predation, hydrodynamic efficiency and their influence on school structure. Environmental Biology of Fishes, The Hague, 13 (3), 195-202.
- Abramovitch, R., & Grusec, J. (1978). Peer imitation in a natural setting. Child Development, 49, 60-65.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49, 227-265.
- Aoki, I. (1982). A simulation study on the schooling mechanism in fish. Bulletin of the Japanese Society of Scientific Fisheries, 48 (8), 1081-1088.
- Asendorpf, J.B., & Baudonnière, P.-M. (1993). Self-awareness and other-awareness: mirror self-recognition and synchronic imitation among unfamiliar peers. Developmental Psychology, 29 (1), 88-95.
- Asendorpf, J.B., Warkentin, V., & Baudonnière, P.-M. (1996). Self-awareness and other awareness II: Mirror self-recognition, social contingency awareness, and synchronic imitation. Developmental Psychology, 32 (2), 313-321.
- Au, W.W.L., & Moore, P.W.B. (1984). Receiving beam patterns and directivity indices of the Atlantic bottlenose dolphin (*Tursiops truncatus*). Journal of the Acoustical Society of America, 75, 255-262.

- Azuma, T., & Iwata, M. (1994). Influences of illumination intensity on the nearest neighbour distance in coho salmon, *Oncorhynchus kisutch*. Journal of Fish Biology, 45 (6), 1113-1118.
- Bateson, G. (1974). Observations of a cetacean community. In J. McIntyre (Ed.), Mind in the Waters (pp. 146-169). New York: Charles Scribner's Sons.
- Baudonnière, P.-M. (1988). Evolution in mode of social exchange in 2, 3, and 4 year old peers. European Bulletin of Cognitive Psychology, 8, 241-263.
- Bauer, G.B., & Johnson, C.M. (1994). Trained motor imitation by bottlenose dolphin (*Tursiops truncatus*). Perceptual & Motor Skills, 79 (3, Pt 1), 1307-1315.
- Bavelas, J.B., Black, A., Lemery, C.R., & Mullett, J. (1986). I *show* how you feel: Motor mimicry as a communicative act. Journal of Personality and Social Psychology, 50, 322-329.
- Bel'kovich, V.M. (1991). Herd structure, hunting, and play: Bottlenose dolphins in the Black Sea. In K. Pryor and K. Norris (Eds.), Dolphin Societies: Discoveries and Puzzles (pp. 17-78). Berkeley, CA: University of California Press.
- Berner, T.O., & Grubb, T.C., Jr. (1985). An experimental analysis of mixed-species flocking in birds of deciduous woodland. Ecology, 66 (4), 1229-1236.
- Bernier, F.J., Reznick, S., & Rosenthal, R. (1988). Synchrony, pseudosynchrony, and dissynchrony: Measuring the entrainment process in mother-infant interactions. Journal of Personality and Social Psychology, 54 (2), 243-253.

- Bisther, A., & Vongraven, D. (1995). Studies of the social ecology of Norwegian killer whales (*Orcinus orca*). In A.S. Blix, L. Walløe, & Ø. Ulltang (Eds.), Whales, Seals, Fish and Man (pp. 169-176). New York: Elsevier North Holland.
- Boyd, G.L., & Parsons, G.R. (1998). Swimming performance and behavior of golden shiner, *Notemigonus crysoleucas*, while schooling. Copeia, *2*, 467-471.
- Breder, C.M., Jr. (1965). Vortices and fish schools. Zoologica, *50*, 97-114.
- Breder, C.M. (1967). On the survival value of fish schools. Zoologica, *52*, 25-40.
- Buck, J. (1988). Synchronous rhythmic flashing of fireflies. The Quarterly Review of Biology, *63*, 265-289.
- Burgess, J.W., & Shaw, E. (1981). Effects of acoustico-lateralis denervation in a facultative schooling fish: A nearest-neighbor matrix analysis. Behavioral and Neural Biology, *33* (4), 488-497.
- Caldwell, M.C., & Caldwell, D.K. (1966). Epimeletic (caregiving) behavior in cetaceans. In K.S. Norris (Ed.), Whales, Dolphins, and Porpoises (pp. 755-789). Berkeley, CA: University of California Press.
- Caro, T.M., & Hauser, M.D. (1992). Is there teaching in nonhuman animals? The Quarterly Review of Biology, *67*, 151-171.
- Cockcroft, V.G., & Ross, G.J.B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R.R. Reeves (Eds.), The Bottlenose Dolphin (pp. 461-478). San Diego, CA: Academic Press.

- Connor, R.C., & Peterson, D.M. (1994). The Lives of Whales and Dolphins. Henry Holt: New York.
- Connor, R.C., Smolker, R.A., & Richards, A.F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). Proceedings of the National Academy of Science, 89, 987-990.
- Connor, R.C., Smolker, R.A., & Richards, A.F. (1992). Dolphin alliances and coalitions. In A.H. Harcourt & F.B.M. de Waal (Eds.), Coalitions and Alliances in Humans and Other Animals (pp. 415-443). Oxford, UK: Oxford University Press.
- Connor, R.C., Wells, R.S., Mann, J., & Read, A.J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R.C. Connor, P.L. Tyack, & H. Whitehead (Eds.), Cetacean Societies: Field Studies of Dolphins and Whales (pp. 91-126). Chicago: University of Chicago Press.
- Crandell, L.E., Fitzgerald, H.E., & Whipple, E.E. (1997). Dyadic synchrony in parent-child interactions: A link with maternal representations of attachment relationships. Infant Mental Health Journal, 18 (3), 247-264.
- Cresswell, W. (1994). Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. Animal Behavior, 47, 433-442.
- Cutts, C.J., & Speakman, J.R. (1994). Energy savings in formation flight of pink-footed geese. Journal of Experimental Biology, 189, 251-261.

- Domenici, P., & Batty, R.S. (1997). Escape behaviour of solitary herring (*Clupea harengus*) and comparisons with schooling individuals. Marine Biology, *128*, 29-38.
- Dudok van Heel, W.H. & Meyer, M.M. (1974). Birth in dolphins (*Tursiops truncatus*) in the Dolphinarium, Harderwijk, Netherlands. Aquatic Mammals, *2* (2), 11-23.
- Dunbar, M.I.M. (1991). Functional significance of social grooming in primates. Folia Primatologia, *57*, 121-131.
- Eastcott, A., & Dickinson, T. (1987). Underwater observations of the suckling and social behavior of a newborn bottlenose dolphin. Aquatic Mammals, *13*, 51-56.
- Eckerman, C.O., & Didow, S.M. (1989). Toddlers' social coordinations: Changing responses to another's invitation to play. Developmental Psychology, *25*, 794-804.
- Eckerman, C.O., & Stein, M.R. (1990). How imitation begets imitation and toddlers' generation of games. Developmental Psychology, *26*, 370-378.
- Eckerman, C.O., Davis, C.C., & Didow, S.M. (1989). Toddlers' emerging ways of achieving social coordinations with a peer. Child Development, *60*, 440-453.
- Elgar, M.A. (1987). Food intake rate and resource availability: flocking decisions in house sparrows. Animal Behavior, *35*, 1168-1176.
- Elgar, M.A., & Catterall, C.P. (1981). Flocking and predator surveillance in house sparrows: Test of an hypothesis. Animal Behaviour, *29* (3), 868-872.

- Essapian, F.S. (1953). The birth and growth of a porpoise. Natural History, *62*, 392-299.
- Feldman, R., & Greenbaum, C.W. (1997). Affect regulation and synchrony in mother-infant play as precursors to the development of symbolic competence. Infant Mental Health Journal, *18* (1), 4-23.
- Feldman, R., Greenbaum, C.W., & Yirmiya, N. (1999). Mother-infant affect synchrony as an antecedent of the emergence of self-control. Developmental Psychology, *35* (1), 223-231.
- Fouts, G.T., Waldner, D.N., & Watson, M.W. (1976). Effects of being imitated and counterimitated on the behavior of preschool children. Child Development, *47* (1) 172-177.
- Gallego, A., & Heath, M.R. (1994). The development of schooling behaviour in Atlantic herring *Clupea harengus*. Journal of Fish Biology, *45*, 569-588.
- Griffiths, S.W. (1997). Preferences for familiar fish do not vary with predation risk in the European minnow. Journal of Fish Biology, *51*, 489-495.
- Grubb, T.C., Jr. (1987). Changes in the flocking behavior of wintering English titmice with time, weather and supplementary food. Animal Behavior, *35*, 794-806.
- Grusec, J., & Abramovitch, R. (1982). Imitation of peers and adults in a natural setting: A functional analysis. Child Development, *53*, 636-642.

- Gubbins, C., McCowan, B., Lynn, S.K., Hooper, S., & Reiss, D. (1999). Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. Marine Mammal Science, 5 (3), 751-765.
- Hanson, F.E., Case, J.F., Buck, E., & Buck, J. (1971). Synchrony and flash entrainment in a New Guinea firefly (*Pteroptyx*). Science, 174, 161-164.
- Harley, H.E., Xitco, M.J., Jr., Roitblat, H.L., & Herman, L.M. (1998). Imitation of human models by bottlenose dolphins. Poster session presented at the Napoli Social Learning Conference, Naples, Italy.
- Harrison, R.J. (1969). Reproduction and Reproductive Organs. In H.T. Andersen (Ed.), The Biology of Marine Mammals (pp. 253-348). New York: Academic Press.
- Harrist, A.W., Pettit, G.S., Dodge, K.A., & Bates, J.E. (1994). Dyadic synchrony in mother-child interaction: Relation with children's subsequent kindergarten adjustment. Family Relations, 43, 417-424.
- Hasegawa, E., & Soeda, H. (1985). Mutual relationship among individuals composing a fish school [Abstract]. Bulletin of the Japanese Society of Scientific Fisheries/Nissuishi, 51 (12), 1921-1926.
- Helfman, G.S., & Schultz, E.T. (1984). Social transmission of behavioural traditions in a coral reef fish. Animal Behaviour, 32 (2), 379-384.

- Heppner, F., & Grenander, U. (1990). A stochastic nonlinear model for coordinated bird flocks. In S. Krasner (Ed.), Ubiquity of Chaos (pp. 233-238). Washington, DC: American Association for the Advancement of Science.
- Herman, L.M., Pack, A.A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H.L. Roitblat & L.M. Herman (Eds.), Language and Communication: Comparative Perspectives (pp. 403-442). Hillsdale, NJ: Lawrence Erlbaum.
- Herskin, J., & Steffensen, J.F. (1998). Energy savings in sea bass swimming in a school: Measurements of tail beat frequency and oxygen consumption at different swimming speeds. Journal of Fish Biology, *53* (2), 366-376.
- Higdon, J.J.L., & Corrsin, S. (1978). Induced drag of a bird flock. American Naturalist, *112*, 727-744.
- Hinde, R.A., & Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. Animal Behaviour, *18*, 169-176.
- Hunter, J.R. (1969). Communication of velocity changes in jack mackerel (*Trachurus symmetricus*) schools. Animal Behaviour, *173*, 507-514.
- Isabella, R.A., Belsky, J., & van Eye, A. (1989). Origins of mother-infant attachment: An examination of interactional synchrony during the infant's first year. Developmental Psychology, *25*, 12-21.

Johnson, C.M., & K.S. Norris (1994). Social Behavior. In K.S. Norris, B. Würsig, R.S.

Wells, & M. Würsig (Eds.), The Hawaiian Spinner Dolphin (pp. 243-286).

Berkeley, CA: University of California Press.

Kirsh, S.J., Crnic, K.A., & Greenberg, M.T. (1995). Relations between parent-child affect

and synchrony and cognitive outcome at 5 years of age. Personal Relationships, 2,

187-198.

Köhler, D. (1976). The interaction between conditioned fish and naive schools of juvenile

carp (*Cyprinus carpio*, Pisces). Behavioural Processes, 1 (3), 267-275.

Krause, J. (1993). Transmission of fright reaction between different species of fish.

Behaviour, 127 (1-2), 37-48.

Laland, K.N., & Williams, K. (1997). Shoaling generates social learning of foraging

information in guppies. Animal Behaviour, 53, 1161-1169.

Lang, T.G. (1966). Hydronamic analysis of cetacean performance. In K.S. Norris (Ed.),

Whales, Dolphins and Porpoises (pp. 410-432). Berkeley, CA: University of

California Press.

Lawren, B. (1991). Going with the crowd. National Wildlife, 30 (1), 14-18.

Lazarus, J. (1979a). The early warning function of flocking in birds: An experimental

study with captive quail. Animal Behaviour, 27 (3), 855-865.

- Lazarus, J. (1979b). Flock size and behaviour in captive red-billed weaverbirds(*Quelea quelea*): Implications for social facilitation and the functions of flocking. Behaviour, *71* (1-2), 127-145.
- Lester, B.M., Hoffman, J., & Brazelton, T.B. (1985). The rhythmic structure of mother-infant interaction in term and preterm infants. Child Development, *56*, 15-27.
- Levín, L.E. (1996). Passage order through different pathways in groups of schooling fish, and the diversified leadership hypothesis. Behavioural Processes, *37* (1), 1-8.
- Lissaman, P.B.S., & Schollenberger, C.A. (1970). Formation flight of birds. Science, *168*, 1003-1005.
- Magurran, A.E., & Higham, A. (1988). Information transfer across fish shoals under predator threat. Ethology, *78*, 153-158.
- Manusov, V. (1992). Mimicry or synchrony: The effects of intentionality attributions for nonverbal mirroring behavior. Communication Quarterly, *40*, 69-83.
- Mann, J., & Smuts, B. (1999). Behavioural development of wild bottlenose dolphin newborns. Behaviour, *136* (pt 5), 529-566.
- Masuda, R., & Tsukamoto, K. (1998). The ontogeny of schooling behaviour in the striped jack. Journal of Fish Biology, *52* (3), 483-493.
- May, R.M. (1979). Flight formations in geese and other birds. Nature, *282*, 778-780.

- McBride, A.F., & Hebb, D.O. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. Journal of Comparative and Physiological Psychology, 41, 111-123.
- McBride, A.F., & Kritzler, H. (1951). Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. Journal of Mammalogy, 32 (3), 251-266.
- Metcalfe, N.B. (1984). The effects of mixed-species flocking on the vigilance of shorebirds: Who do they trust? Animal Behavior, 32, 986-993.
- Mikheev, V.N. (1995). Choice between individual schooling behavior in fishes with a facultative social strategy. Journal of Ichthyology, 35 (8), 167-172.
- Moore, B.R. (1996). The evolution of imitative learning. In C.M. Heyes & B.G. Galef, Jr. (Eds.). Social Learning in Animals: The Roots of Culture (pp. 245-265). San Diego: Academic Press.
- Nadel-Brulfert, J., & Baudonnière, P.M. (1982). The social function of reciprocal imitation in 2-year-old peers. International Journal of Behavioral Development, 5, 95-109.
- Niwa, H.-S. (1996). Newtonian dynamical approach to fish schooling. Journal of Theoretical Biology, 181, 47-63.
- Nonacs, P., Smith, P.E., & Mangel, M. (1998). Modeling foraging in the northern anchovy (*Engraulis mordax*): Individual behavior can predict school dynamics

- and population biology. Canadian Journal of Fisheries and Aquatic Sciences, 55 (5), 1179-1188.
- Norris, K.S., & Dohl, T.P. (1980). The structure and functions of cetacean schools. In L.M. Herman (Ed.), Cetacean Behavior: Mechanisms and Functions (pp. 211-261). New York: John Wiley & Sons .
- Norris, K.S., & Johnson, C.M. (1994). Schools and Schooling. In K.S. Norris, B. Würsig, R.S. Wells, & M. Würsig (Eds.), The Hawaiian Spinner Dolphin (pp. 232-242). Berkeley, CA: University of California Press.
- Norris, K.S., & Prescott, J.H. (1961). Observations of Pacific cetaceans of Californian and Mexican waters. University of California Publications in Zoology, 63, 291-402.
- Parrish, J.K. (1988). The costs and benefits of schooling in fish. Unpublished doctoral dissertation, Duke University.
- Partridge, B.L. (1981). Lateral line function and the internal dynamics of fish schools. In W.N. Tavolga, A.N. Popper, & R.R. Fay (Eds.), Hearing and Sound Communication in Fishes (pp. 515-522). Springer-Verlag: New York.
- Partridge, B.L. (1982a). Rigid definitions of schooling behaviour are inadequate. Animal Behaviour, 30 (1), 298-299.
- Partridge, B.L. (1982b). The structure and function of fish schools. Scientific American, 246 (6), 114-123.

- Partridge, B.L., & Pitcher, T.J. (1980). The sensory basis of fish schools: Relative roles of lateral line and vision. Journal of Comparative Physiology, 135, 315-325.
- Peddemors, V.M. (1990). Respiratory development in a captive-born bottlenose dolphin (*Tursiops truncatus*) calf. South Africa Journal of Zoology, 25, 178-184.
- Peddemors, V.M., Fothergill, M.A.W., & Cockroft, V.G. (1992). Feeding and growth in a captive-born bottlenose dolphin, *Tursiops truncatus*. South African Journal of Zoology, 27, 74-80.
- Pitcher, T.J., & Parrish, J.K. (1993). Functions of shoaling behaviour in teleosts. In T.J. Pitcher (Ed.), Behaviour of teleost fishes (pp. 363-439). New York: Chapman and Hall.
- Pitcher, T.J., Partridge, B.L., & Wardle, C.S. (1976). A blind fish can school. Science, 194, 963-965.
- Pomeroy, H., & Heppner, F. (1992). Structure of turning in airborne rock dove (*Columba livia*) flocks. Auk, 109 (2), 256-267.
- Potts, W.K. (1984). The chorus line hypothesis of manoeuvre coordination in avian flocks. Nature, 309, 344-345.
- Pryor, K., & Shallenberger, I. (1991). Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the eastern tropical Pacific. In K.

- Pryor & K. Norris (Eds.), Dolphin Societies: Discoveries and Puzzles (pp. 161-198). Berkeley, CA: University of California Press.
- Pulliam, H.R. (1973). On the advantages of flocking. Journal of Theoretical Biology, 38, 419-422.
- Ray, R.D., Carlson, M.L., Calson, M.A., Carlson, T.M., & Upson, J.D. (1986). Behavioral and respiratory synchronization quantified in a pair of captive killer whales. In B.C. Kirkevold & J.S. Lockard (Eds.), Behavioral Biology of Killer Whales (pp. 135-147). New York: Alan R. Liss, Inc.
- Reid, K., Mann, J., Weiner, J.R., & Hecker, N. (1995). Infant development in two aquarium bottlenose dolphins. Zoo Biology, 14, 135-147.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. Animal Behaviour, 51, 1077-1086.
- Roberts, M.C., Santogrossi, D.A., & Thelen, M.H. (1980). The effects of being imitated on adult attraction to children. Journal of Social Psychology, 111 (2), 253-258.
- Romey, W.L. (1996). Individual differences make a difference in the trajectories of simulated schools of fish. Ecological Modelling, 92, 65-77.
- Ross, H.S. (1982). Establishment of social games among toddlers. Developmental Psychology, 18, 509-518.
- Rowe, D.M., & Denton, E.J. (1997). The physical basis for reflective communication between fish, with special reference to the horse mackerel, *Trachurus trachurus*.

Philosophical Transactions of the Royal Society of London B: Biological Sciences, 352(1353), 531-549.

Ryer, C.H., & Olla, B.L. (1991). Information transfer and the facilitation and inhibition of feeding in a schooling fish. Environmental Biology of Fishes, 30(3), 317-324.

Saayman, G.S., Tayler, C.K., & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* ehrenburg). Behaviour, 44, 212-233.

Sadedin, S.R., & Elgar, M.A. (1998). The influence of flock size and geometry on the scanning behaviour of spotted turtle doves, *Streptopelia chinensis*. Australian Journal of Ecology, 23(2), 177-180.

Schroeder, J.P. (1990). Breeding bottlenose dolphins in captivity. In S. Leatherwood & R.R. Reeves (Eds.), The Bottlenose Dolphin (pp. 435-446). San Diego, CA: Academic Press.

Smeets, P.M., & Kauffman, J.M. (1983). On children being imitated: Predictability of reinforcement by the observer's imitations. Journal of Genetic Psychology, 142(1), 135-142.

Stern, D. (1977). The First Relationship: Mother and Infant. Cambridge, MA: Harvard University Press.

Stewart, I. (1991). Mathematics: All together now Nature, 350, 557.

- Stewart, I. (1999). The synchronicity of firefly flashing. Scientific American, 280 (3), 104-106.
- Strogatz, S.H., & Stewart, I. (1993). Coupled oscillators and biological synchronization. Scientific American, 269 (6), 102.
- Tavolga, M.C. (1966). Behavior of the Bottlenose dolphin (*Tursiops truncatus*): Social interactions in a captive colony. In K.S. Norris (Ed.), Whales, Dolphins, and Porpoises (pp. 718-730). Berkeley, CA: University of California Press.
- Tavolga, M.C., & Essapian, F.S. (1957). The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zooligica, 42 (3), 11-34.
- Tayler, C.K., & Saayman, G.S. (1973). Imitative behavior by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. Behaviour, 44 (3-4), 277-298.
- Thelen, M.H., & Kirkland, K.D. (1976). On status of being imitated: effects on reciprocal imitation. Journal of Personality and Social Psychology, 33, 691-697.
- Thelen, M.H., Dollinger, S.J., & Roberts, M.C. (1975). On being imitated: Its effects on attraction and reciprocal imitation. Journal of Personality and Social Psychology, 31, 467-472.
- Triossi, F., Pace, D.S., Terranova, M.L., & Renzi, P. (1998). The development of suckling behavior in two captive-born calves of bottlenose dolphins (*Tursiops truncatus*). Aquatic Mammals, 24 (3), 75-83.

- Tronick, E., Als, H., & Brazelton, T.B. (1980). Monadic phases: A structural descriptive analysis of infant-moter face-to-face interaction. Merrill-Palmer Quarterly, 26, 3-24.
- Vabø, R., & Nøttestad, L. (1997). An individual based model of fish school reactions: Predicting antipredator behaviour as observed in nature. Fisheries Oceanography, 6(3), 155-171.
- Vergara, V.E., & Levín, L.E. (1982). Group vs. individual in the acquisition of an avoidance response in schooling fish. Acta científica venezolana, Caracas, 33 (3), 258-262.
- Waltz, E.C. (1987). A test of the information-centre hypothesis in two colonies of common terns, *Sterna hirundo*. Animal Behaviour, 35 (1), 48-59.
- Ward, P., & Zahavi, A. (1973), The importance of certain assemblages of birds as “information-centres” for food-finding. Ibis, 115, 517-534.
- Weih, D. (1973). Hydromechanics of fish schooling. Nature, 241, 290-291.
- Weih, D. (1975). Some hydrodynamical aspects of fish schooling. In T. Wu, C.J. Brokaw, & C. Brennen (Eds.), Swimming and Flying in Nature (pp. 703-718). New York: Plenum Press.
- Wells, R.S. (1991). Bringing up baby. Natural History, 100 (8), 56-62.

- Wells, R.S., Irvine, A.B., & Scott, M.D. (1980). The social ecology of inshore odontocetes. In L.M. Herman (Ed.), Cetacean Behavior: Mechanisms and Functions (pp. 263-317). New York: John Wiley & Sons.
- Whipple, E.E., Fitzgerald, H.E., & Zucker, R.A. (1995). Parent-child interactions in alcoholic and nonalcoholic families. American Journal of Orthopsychiatry, 65 (1), 153-159.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral and Ecological Sociobiology, 38, 237-244.
- Wickelgren, I. (1990). Chaos in the flock. Discover, 11 (6), 28.
- Williams, T.M., Friedl, W.A., Fong, M.L., Yamada, R.M., Sedivy, P., & Haun, J.E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature, 355, 821-823.
- Xitco, M.J., Jr., & Roitblat, H.L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. Animal Learning & Behavior, 24 (4), 355-365.
- Xitco, M.J., Jr., Harley, H.E., & Brill, R.L. (1998). Action level imitation by bottlenose dolphins. Poster session presented at the Napoli Social Learning Conference, Naples, Italy.
- Zhuikov, A.Yu., & Pyanov, A.I. (1993). Mutual influence of individuals with different learning performance in exploratory behavior of the fish Buenos Aires Tetra

(*Hemigrammus caudovittatus*, Characinidae). Russian Journal of Aquatic

Ecology, 2 (2), 131-134.