Studying Dolphin Behavior in a Semi-Natural Marine Enclosure: Couldn't we do it all in the Wild?

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Studying Dolphin Behavior in a Semi-Natural Marine Enclosure: Couldn't we do it all in the Wild?

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The study of marine mammals in the wild is faced with major difficulties: encounter frequency and duration are limited, individual identification is difficult, social behaviors occur mostly in murky or deep water, the ability to assign vocalizations to individuals is usually very limited, sea conditions are not always suitable for research, and the design of controlled experiments is virtually impossible. In contrast, research in captivity poses different methodological obstacles due to confined space, artificial and sometimes poor environments, forced social structure, small sample sizes, subjects that are not always good representatives of wild populations etc., all provide constant challenge to scientists. This paper reviews some of the studies on Black Sea bottlenose dolphins (*Tursiops truncatus ponticus*) conducted during the 15 years since the establishment of the International Laboratory for Dolphin Behaviour Research (ILDBR) located at the semi-natural Dolphin-Reef (Eilat, Israel) tourist facility. We describe how this site overcomes many of the problems that characterize captivity sites, and how our research gains important insight into dolphin behavior, which is difficult to obtain – if at all – in the study of wild populations. We conclude that studies of captive and wild dolphins can complement each other for a better understanding of dolphin behavior.

Behavioral research of wild terrestrial animals is hampered by a broad range of obstacles: (1) encounter frequency of animals and the duration of such encounters are usually limited, especially when non-habituated subjects are affected by the presence of humans; (2) individual identification is typically labor-intense, and it either takes substantial time and effort during repeated encounters until identification skills are acquired by the researchers, or it involves individual tagging which might harm the tagged animals; and (3) the design of experiments is susceptible to the influence of many uncontrolled variables, including the concern that research itself alters the studied behaviors (Deecke, 2006; Fusani, Canoine, Goymann, Wikelski, & Hau, 2005; Gannon & Sikes, 2007).

As much as research on land can be complicated, the marine environment further enhances these complications: due to the vast spatial dimensions and the lack of clearly recognizable habitat boundaries, encounter frequency and observation duration are further decreased, and individual identification is harder. In addition, problems that are more specific to the marine environment further limit such research: the animals spend most of their time underwater – frequently in murky or deep water, whereas scientists are usually limited to the water surface, which bounds continuous tracking of behaviors; and even underwater video equipment is still constrained by water visibility of 20-40 m at best. Acoustics helps in tracking unobserved animals but has its own limitations and physical complications. For example, the ability to assign specific vocalizations to emitting individuals in open water is usually very limited. In addition, weather and sea conditions are not always suitable for long-lasting and continuous observations (Deecke, 2006; Herzing, 1996; Janik, 2009; Todt & Veit, 2005).

In contrast, although research of marine mammals in captivity can easily overcome the above difficulties, it poses different obstacles: (1) the animals are kept, sometimes in high densities, in a confined space – much smaller than their natural home range; (2) the environment is often artificial and poor, and thus lacks sufficient stimuli for animals known by their high intelligence and curiosity (see Marino et al., 2008); (3) social structure is usually artificial, and dictated mostly by maintenance concerns such as the reduction of aggression between rivals, rather then by the need to retain natural grouping characteristics; and (4) passive feeding and medical treatment (e.g., hormones) further modify the behaviors of captive animals. As a consequence, research in captivity results in small sample sizes of doubtful representatives of wild populations. This may put in question the external validity of behavioral findings, and provides constant challenges to overcome these obstacles in order to conduct meaningful and insightful research (Fusani et al., 2005; Rose, Parsons, & Farinato, 2009; Waples & Gales, 2002). Nonetheless, whereas the importance of studying the behavior of captive terrestrial animals – even apes – has been broadly recognized (e.g., de Waal, 1989, 1996, 2000; de Waal & Lanting, 1997), such research of marine mammals is still in debate (Rose et al., 2009).

Here, we review some of the studies conducted over 15 years of research on Black Sea bottlenose dolphins (*Tursiops truncatus ponticus* Barabasch-Nikiforov, 1940) at the International Laboratory for Dolphin Behaviour Research (ILDBR) located at the Dolphin-Reef tourist facility in Eilat, Israel. We highlight how our studies of a captive group provide insights into bottlenose dolphin behavior, which are – if at all possible – very difficult to obtain from wild dolphin populations. We also discuss how one can overcome, or at least confine, many of the abovementioned drawbacks that limit research in artificial captivity sites.

The current paper reviews only studies published in peer-reviewed journals. Additional information on the development of vocalizations in calves (Bojanowski, 2002; Bojanowski, Veit, & Todt, 2000), novel context-dependent vocalizations during agonistic interactions and stress (Veit, 1999, 2002; Veit, Bojanowski, Todt, Zilber, Supin, & Mukhametov, 1997), further data from

playback experiments (van der Woude, 2003), and conclusions from translocation events (Veit, 2002; Veit et al., 1997), are yet to be published.

The Dolphin Reef Site

The ILDBR is located in a tower about 8 m above a 14,000 m^2 continuous semi-natural marine enclosure, the "Dolphin-Reef" tourist facility (Fig. 1). The site is located south of the city of Eilat, Israel, at the northern part of the Gulf of Aqaba, the Red Sea (34°56'13"E/29°31'37"N; for a location map see Perelberg & Schuster, 2008). The enclosure is a sandy bottom marine habitat with scattered natural patches of sea grass beds and coral knolls, and enriched with several artificial reef constructions. The bottom gradually slopes from the shore to about 15-20 m depth along a plastic circumference net, which allows free in- and out-flow of sea water and marine organisms such as fish, cephalopods, jellyfish and occasional sea turtles, the latter squeezing themselves under the net. Visibility both underwater and from the ILDBR observation tower is usually very good year round (up to 25 m underwater, see Fig. 1). The measures of both surface area/animal and water volume/animal at the Dolphin Reef put it as one of the top of cetacean facilities in the world (Couquiaud, 2005).

Figure 1. The Dolphin Reef site: a) Dolphin enclosure. b) Tourist swimming beach (no dolphins). c) Tourist pier. d) ILDBR tower. e) Trainer facilities. f) Open sea. Picture provided by S. E. van der Woude (taken by Omer Armoza as requested).

Between the years 1997 to 2002, one or two underwater gates were open to the sea all year round, usually 24 hr/day, enabling the dolphins almost unlimited access to the open sea. Most males (adult and adolescent) and the adolescent females frequently went into the open sea, and always returned back to the enclosure. During this period, there was only one event of a nine days long-excursion of an adolescent male (Lemon, see Fig. 2), who was identified in Dahab, (Sinai, Egypt), about 125 km to the south, after which he returned back to the Dolphin Reef. All other excursions lasted less than a day. However, due to unsupervised encounters between humans and dolphins along the public beaches of Eilat, which led to harassment of the dolphins by humans and resulting in aggressive dolphin behaviors, the gates were closed and the dolphins were confined to the enclosure ever since. The species (*T. truncatus*), although of a different local subspecies, is common in the Red Sea, but rarely seen at the northern part of the Gulf of Aqaba along the beaches of Eilat (Feingold, 2006). A sister species – the Indo-Pacific bottlenose dolphin (*T. aduncus*, which is actually believed to be closer to the *Stenella* and *Delphinus* genuses, see LeDuc, Perrin, & Dizon, 1999), as well as four other cetacean species, occasionally visit the northern tip of the gulf (Feingold, 2006), and sometimes interact with the Dolphin Reef dolphins through the circumference net (ILDBR, unpublished data).
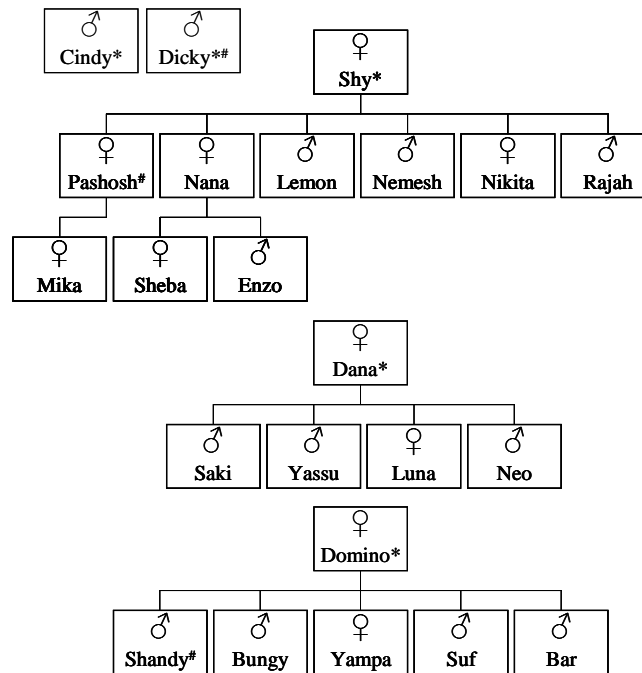
Figure 2. Maternal lineages of the dolphins at the Dolphin Reef, Eilat. Two males and three females (denoted with *) were transferred in 1990 from the Black Sea and compose the initial group. Three dolphins were transferred back to the Black Sea (denoted with #): Dicky in 1996; Shandy and Pashosh in 2004. Cindy possibly fathered all offspring, but fatherhood by Dicky and Shandy when reaching sexual maturity (before their translocation) can not be excluded.

The non-subdivided enclosure allows the dolphins unrestricted social interactions and associations among representatives of all age and sex categories (except for rare separations for care-giving reasons). The dolphins prey on fish and invertebrates inside the enclosure (and used to hunt in the open sea when the gates were open) as a supplement of daily feeding and an expression of their natural behaviors. Artificial feeding, which is the primary food source, is provided by the trainers five times a day (at 9:00, 10:00, 12:00, 14:00, and 16:00 hr) from designated platforms along the floating tourist pier (see Fig. 1c). The early morning feeding is closed to the public and used to monitor the dolphins' health and for training of medical procedures, which is the only case in which training is reinforced by food. Since the construction of the floating pier in 2001, feeding is not contingent on performing any behaviors for show, and the dolphins never display any show related behaviors before or during feeding. Training sessions are performed after feedings as a tourist attraction and a means of environmental and social enrichment for the dolphins. These include individually performed simple tricks such as leaping out of the water or emitting of above-water sounds. Dolphin participation is completely voluntary, and food reward is never provided or related to such training. Only human attention by means of vocal cheers, applause, and petting by the trainer are used as reinforcers for dolphin performance.

Three fully guided and supervised programs for tourists take place between feeding times: swimming with dolphins, diving with dolphins, and dolphin assisted therapy. Since the establishment of the Dolphin Reef, participation by the dolphins in all these programs has always been voluntary, spontaneous and not reinforced by food. Dolphins are free to approach any person, and have free access to large shelter areas inside the enclosure that are prohibited to humans. Tourists, on the other hand, are not permitted to chase after, harass or touch the dolphins. Housing conditions of the dolphins comply with the (currently suspended) Animal and Plant Health Inspection Service (APHIS, 2001) swim-with-the-dolphin program regulations. Studies were approved by the corresponding universities' ethical committees for experiments on animals, following Israeli legal regulations.

The Dolphins

The initial dolphin group consisted in 1990 of two males and three females brought from Taman Bay (Black Sea, Russia), under an agreement with the Severtsov Institute in Moscow. All additional animals were descendants of the initial group (Fig. 2). During the 15 years since the establishment of the ILDBR in 1994, the composition of the dolphin group varied due to new births, deaths, and translocation of three dolphins back to the Black Sea. At times, the group was composed of all age and sex classes: adults (sexually mature males and females), adolescents (between 6 and 10 years of age, that had yet to sire offspring), juveniles (from weaning until 6 years old), and calves (from birth to weaning at the age of 18-20 months). A detailed description of the group composition can be found in each of the corresponding studies (Perelberg & Schuster, 2008, 2009; Todt & Veit, 2005; van der Woude, 2008, 2009). Individual identification of the

dolphins is based on distinct shapes and marks of dorsal fins, as well as body size, girth, color and individual body marks.

Acoustic Studies

This paper reviews some of the acoustic studies conducted at ILDBR on the temporal and syntactical structure as well as the behavioral contexts of dolphin vocalizations during agonistic and affiliative interactions (for recent general reviews, definitions and categorization of dolphin vocalizations see Janik, 2009; van der Woude, 2009). Other studies examined the effects of anthropogenic noise on dolphin behavior from a geophysical survey (van der Woude, 2008), and vessel engines (ongoing). Depending on the specific requirements of each study, underwater and above-water video, as well as underwater hydrophones were used. Detailed descriptions of methods can be found in each of the corresponding studies (Todt & Veit, 2005; van der Woude, 2008, 2009).

Vocalizations related to anticipation of positive experiences

A newly discovered vocalization is a tonal low-frequency sound termed 'moan' (van der Woude, 2009). To our knowledge, moan fundamental frequencies (39-406 Hz) are by far the lowest described for tonal vocalizations of toothed whales, but similar to those of baleen whales. Moans are clearly distinct from any other vocalization type reported for this species in frequency, duration (0.2-8.7 sec), and structure (non-patterned contour; see Fig. 3). All acoustic recordings made by van der Woude between 2002-2009 contained moans, although these vocalizations were extremely rare: 68 hours recorded with a spacious two-dimensional hydrophone array over the course of four months, contained only 132 unambiguous moans. Of these moans, 49 were accompanied with the release of a bubble-stream from the dolphin's blowhole which allowed for the identification of the moaner. While all animals but one adult female (Shy) moaned, the majority of moans was produced by three females (an adult – Nana, and two adolescents – Yampa and Luna). Most moans occurred prior to either feeding or petting by trainers and were therefore suggested to indicate anticipation of a human-supplied positive experience (van der Woude, 2009).
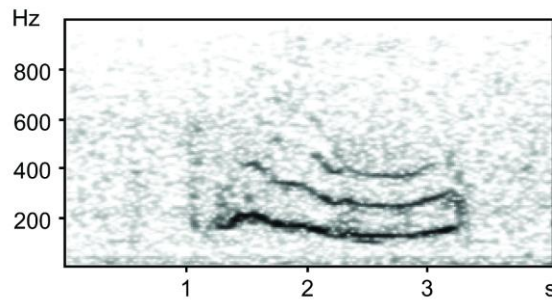
Hz

800

600

400

200

1   2   3   s

Figure 3. Spectrogram of a 'moan'. Moans are low-frequency tonal sounds, typically accompanied by the release of a bubble-stream from the dolphin's blowhole, and produced prior to an expected positive hedonic experience.

Patterns of responses to vocalizations

Burst-pulse sounds (bursts) were studied by analyzing underwater video and audio recordings of ten dolphins (adults: 1 male, 3 females; juveniles: 2 males, 2 females; calves: 2 males). Bursts were responded to only by bursts, with a short latency (ca. 0.2 s), and with the dominance rank dictating the roles: the subordinate subject responding to the dominant initiator (Todt & Veit, 2005).

Responses to whistles were studied on the same ten dolphins as above, by conducting playback experiments. As with bursts, both visible movements and acoustic responses were dependent on dominance rank, where the dominant male responded generally stronger to the stimuli than other group members, especially when the signature whistle of its former opponent – that was translocated to the Black Sea years before the experiments took place – was played (Todt & Veit, 2005).

These findings highlight the usually neglected importance of the temporal characteristics of emitted vocalizations. While agonistic behavior in other animal species is typically characterized by overlapping vocalizations of opponents (Hultsch & Todt, 1982; Todt & Naguib, 2000), these studies demonstrated that bursts were characterized instead by coordinated turn-taking, that question the assumed agonistic context suggested for bursts. In contrast, signature whistles that are believed to function as contact calls (Janik & Slater, 1998), overlapped between opponents, and might as well serve as agonistic signals (Todt & Veit, 2005).

Social Behavior Studies

The bottlenose dolphin is known as a highly social species, in which cooperative behaviors construct a large part of its behavioral repertoire, including communal foraging and hunting (Connor, Wells, Mann, & Read, 2000; Gazda, Connor, Edgar, & Cox, 2005; Reynolds, Wells, & Eide, 2000; Shane, 1990), defense against predators and conspecifics (Reynolds et al., 2000), vigilance sharing (Gnone, Benoldi, Bonsignori, & Fognani, 2001), alliances for mating

purposes (Connor & Mann, 2006; Connor et al., 2000), and play behaviors (Bel'kovich, 1991). Captive bottlenose dolphins are therefore good candidates for the detailed study of cooperative behaviors under more controlled conditions.

Evolutionary approaches that address the ultimate processes by which cooperation develops and maintains in a population over consecutive generations, are not always sufficient to explain the proximate processes that lead to the occurrence of cooperation, especially in cases where a cooperation bias is observed, i.e., when cooperation occurs despite non-cooperation being immediately more beneficial. Two studies took advantage of the housing conditions at the Dolphin Reef to address the ultimate and proximate processes that eventually lead to the development of cooperation. The condition of all age and sex classes living together in a single large enclosure, allowed us to study the influences of social relationships on the tendency of the dolphins to conduct cooperative behaviors in two separate contexts: coordinated breathing and coordinated petting by human staff (Perelberg & Schuster, 2008, 2009).

Breathing synchrony

Coordinated breathing does not represent any distinctive cooperative behavior in itself. Rather, it is linked to other coordinated acts such as cooperative foraging/hunting, resting, aggression, consorting females, and playing. It can also reveal both short-term context-dependent associations, and long-lasting relationships such as between mothers and calves or within male alliances (reviewed in Perelberg & Schuster, 2008). Coordinated breathing thereby offers an indirect measure that is objective, discrete, unambiguous and easily observed from above the water (Hastie, Wilson, Tufft, & Thompson, 2003).

During 140 observation sessions of association patterns (2,840 min), and 73 observation sessions of dyadic breathing (3,969 recorded events during 3,856 min), a strong link was found between the dyadic coordination levels and the association patterns of the 13 studied dolphins (adults: 1 male, 4 females; adolescents: 2 males, 2 females; calves: 2 males, 2 females), when both age/sex categories and spatial formation were considered. As expected, the highest breathing synchrony was found between mother-calf pairs (Perelberg & Schuster, 2008), in agreement with the hydrodynamic advantages that calves gain from swimming in either infant or echelon positions (Noren, Biedenbach, Redfern, & Edwards, 2008; Weihs, 2004). But adolescent pairs, and especially the adolescent male pair that presented equivalent strong association levels to the mother-calf pairs, were similarly synchronized in breathing, despite their parallel swimming formation (Perelberg & Schuster, 2008), which is the worst hydrodynamic formation (Weihs, 2004), and thus provided no recognizable immediate advantage. This was suggested to represent an example of a cooperation bias, as will be discussed below (Perelberg & Schuster, 2008).

Coordination during petting by human guides

The voluntary nature of human-dolphin interactions at the Dolphin Reef as described above, allowed us to treat the approaches of the dolphins to the human guides to receive petting as a desired resource (Brensing, 2005; Brensing & Linke, 2004; Brensing, Linke, Busch, Matthes, & van der Woude, 2005) which was possibly open for competition, and which the dolphins could consume either alone or in a pair. The analysis of the underwater video recordings (about 2,800 min from 392 scuba diving sessions) revealed that dolphins preferred petting in pairs, even though coordinated pair petting was more difficult to maintain than solitary petting, and petting amount was also shared among the dyad. Therefore, dolphins presented a cooperation bias, in which the social component of paired petting compensated for the reduced total petting time in comparison to solitary petting (Perelberg & Schuster, 2009).

Both of the above studies (Perelberg & Schuster, 2008, 2009) provided evidence for the effect of social relationships on the establishment and maintenance of cooperative behaviors in bottlenose dolphins, and contrasts with an economic perspective based on immediate material outcomes alone. Cooperation bias can then be explained by suggesting that proximate processes that evoke performance include not only immediate material reinforcements, but also affective states induced by the social context of cooperation. Affective states act as additional reinforcements, especially when material reinforcements are absent or long-delayed. Affective states can then be adaptive by strengthening social relationships (e.g., breathing synchrony of adolescent males), which can lead to lifetime probabilistic gains in fitness (Perelberg & Schuster, 2008, 2009; Schuster, 2002; Schuster & Perelberg, 2004).

Dolphin Welfare

Human-dolphin interactions

Swim-With-The-Dolphins (SWTD) and especially Dolphin-Assisted-Therapy (DAT) programs proliferate worldwide, both in the wild and in captivity. Originating from interactions with wild dolphins at sea (Dobbs, 1977, 1981, 1990), DAT rapidly moved to locations where interactions can be planned, timed, and well supervised for the benefit of the patient. DAT was reported to have positive effects in cases of autism (Smith, 1978), mental retardation, and emotional or mental problems (Nathanson, 1989; Nathanson & de Faria, 1993). Nicole Kohn (2004) performed a multi sites comparative study where she found that emotional, cognitive, and social improvements in treated children improved significantly. However, other researchers challenge the effectiveness of DAT over other therapies, including hydrotherapy and therapy assisted by domesticated animals (Brensing, 2005; Marino & Lilienfeld, 1998, 2007).

Whereas most DAT studies focused on the effects on the participating humans (for reviews see Humphries, 2003; Kohn, 2004; Marino & Lilienfeld,

1998, 2007), much less attention has been given to the effects on the behavior of the dolphins. Since both DAT and SWTD are provided by the Dolphin Reef facility, it was possible to study these effects in comparison to another facility, the Dolphins Plus (Key Largo, Florida, USA), which is also a fenced marine enclosure, but with a considerable smaller surface area (about 600 m^2) and much shallower (about 5 m). In addition, in contrast to the Dolphin Reef, at Dolphins Plus there were no shelter areas available for the dolphins where human access was prohibited during the interactions (Brensing, 2005; Brensing & Linke, 2004; Brensing et al., 2005).

While assessing the possible effects SWTD and DAT on the dolphins, the spatial distribution of dolphins in the presence and absence of human swimmers were compared in both sites, and contrasted with random spatial distribution (83 sessions with five dolphins at Dolphins Plus, and 37 sessions with 13 dolphins at the Dolphin Reef). At both sites, swims were guided by local staff, and not reinforced with food. Therefore, dolphin interactions with humans were motivated by the human presence alone. Results revealed that dolphins' responses to the presence of swimmers differed between the two sites. At Dolphins Plus, dolphins showed avoidance behaviors, expressed as increasing their distance from humans – more than expected by chance, and increasing their swim speed, diving depth and breathing frequency – in comparison to the control condition of no swimmers in the water. In contrast, dolphins at Dolphin Reef showed an opposite response – they approached swimmers and spent longer time in their vicinity – than expected by chance, even though they were free not to do so (Brensing, 2005; Brensing & Linke, 2004; Brensing et al., 2005). Hence, these studies provide an additional support to the notion that enclosure conditions have an important role on the welfare of captive dolphins, namely: the depth, size and water volume of the holding facility; the role that shelter areas take in reducing dolphins' stress levels; and the requirement for professional supervision of human-dolphin interactions (see also Samuels & Spradlin, 1995).

Discussion

In general, the advantages of studying bottlenose dolphin behavior at Dolphin Reef include the presence of group members of all age and sex classes in one large marine enclosure, which enabled detailed analysis of social relationships; the habituation of the dolphins to the presence of humans and recording devices and the good visibility of the water which allowed the implementation of different research methods, including the identification of moving and vocalizing individuals; and finally, the presence of the dolphins year-round provided an opportunity to compile large and detailed databases of dolphin behaviors throughout various contexts, reproductive seasons and developmental stages, which is rarely possible when studying wild dolphins.

One such example is the ability to identify both the sender and the contextual use of vocalizations. The function of signature whistles has now been broadly accepted as individual contact calls used for intra-specific recognition

during separation and for reunion (for review see Janik, 2009), indicate levels of arousal or stress (Caldwell, Caldwell, & Tyack, 1990; Esch, Sayigh, Blum, & Wells, 2009), and possibly also as a query signal addressing specific individuals (Janik, 2000b). But apart from signature whistles, the functions of other vocalizations are still generally vague. Janik (2009) reviews current knowledge about context-specific usage of vocalizations, which sums up into three main contexts: (1) aggression: broad-band burst-pulsed sounds in captive (Blomqvist & Amundin, 2004; McCowan, & Reiss, 1995c; Overstrom, 1983) and wild dolphins (Herzing, 1996), and low-frequency narrow-band 'pops' of wild males while consorting females (Connor & Smolker, 1996), which are also used in another wild population while foraging (Nowacek, 2005); (2) play-fight: burst-pulsed sound followed by a narrow-band whistle in a captive group (Blomqvist, Mello, & Amundin, 2005); and (3) food-related low-frequency bray calls (Janik, 2000a; dos Santos, Ferreira, & Harzen, 1995) and 'upsweep' whistles (Herzing, 1996) assumed to function in prey manipulation rather than intra-specific communication (Janik, 2000a).

The analysis of dolphin vocalizations at the Dolphin Reef provided valuable insights into the function of additional sound categories and revealed novel aspects about the structure of information encoding in this species, such as the low-frequency 'moan', which was produced before positive hedonic experiences (van der Woude, 2009). Further research in other captive and wild populations should clarify whether these vocalizations are unique local 'dialects' of the Dolphin Reef group, as reported for killer whales (*Orcinus orca*, see Ford & Fisher, 1983), or a natural part of the species' vocal repertoire, which have been overlooked so far due to their inconspicuousness and scarcity, technical limitations, or methodological biases.

In addition, the structural organization of burst-pulsed sounds and the context within which these were used (Todt & Veit, 2005), put into question the validity of burst-pulsed sounds as uniquely representing agonistic interactions, and supports a broader usage, such as the play-fight behavior reported by Blomqvist et al. (2005). Similarly, the use of signature whistles might have a broader function than previously suggested, to include also agonistic interactions, as proposed by Todt & Veit (2005). Furthermore, the strong responses of the dominant male to the whistle of its long absent rival indicate on exceptional long-term memory capabilities (Todt & Veit, 2005).

The study of social behaviors of bottlenose dolphins in the wild is usually constrained by low encounter frequency and duration, difficult identification of individuals, limited visibility, uncontrolled environment, rough sea conditions, and the possible changes in behavior due to the presence of researchers. Hence, data collection is usually either limited to just a few observations of each individual, or span over many years. Whitehead (2008) estimated that in order to decipher reliable association levels there should be at least 50 observations of each pair, and Gibson and Mann (2008) estimated time for reliable association estimates to be about 10 hr/subject. This criterion is rarely met in short-term (Chilvers & Corkeron, 2001; Gero, Bejder, Whitehead, Mann, & Connor, 2005; Maze-Foley &

Würsig, 2002; Möller, Beheregaray, Allen, & Harcourt, 2006; Rossbach, & Herzing, 1999), medium-term (Lopez & Shirai, 2008; Lusseau et al., 2003; Urian, Hofmann, Wells, & Read, 2009; Wiszniewski, Allen, & Möller, 2009), or even long-term studies of wild dolphin populations (Gibson & Mann, 2008; Lusseau et al., 2006; Rossbach & Herzing, 1999; Wells, 2003). Moreover, the accumulation of infrequent observations over long term might obscure fine scale changes in association levels. The studies of social behaviors conducted at the Dolphin Reef included hundreds of observations of each subject over dozens of observation hours, in a relatively short time that reduced the possibility of temporal changes in associations during the study, and thus were able to reliably reflect the social relationships within the group in a short period in time (Perelberg & Schuster, 2008, 2009). However, caution has to be taken when interpreting social relationships of captive, artificially grouped animals, and validation via comparisons to wild populations (Connor & Mann, 2006; Connor, Smolker, & Bejder, 2006; Connor, Smolker, & Richards, 1992) is required.

This paper does not address the ethical aspects of holding a wild intelligent animal such as the bottlenose dolphin in captivity (Rose et al., 2009), but suggests that as long as these animals are kept in captivity, measures to ensure their best treatment, and both physical and mental welfare, should be taken. By comparing different captivity conditions, a set of guidelines could be devised and enforced to secure these captivity conditions. Features that were identified to be important in sites where SWTD programs exist are: a large water volume per animal and for the group; adequate shelter areas prohibited to human access; controlled and supervised human-dolphin interactions; and the ability of the dolphins to freely choose whether or not to interact with humans (Brensing, 2005; Brensing & Linke, 2004; Brensing et al., 2005). If these conditions are met, captive dolphins often behave similar to wild solitary social dolphins, which initiate contact with humans and many times develop long-term close relationships with familiar people (Goodwin & Dodds, 2008; Wilke, Bossley, & Doak, 2005).

The process, by which signature whistles have been discovered, verified, debated, and reassured, provides an excellent example for the integration and interdependency between studies in captivity and in the wild that advances the understanding of a scientific challenge. It began with pioneering research on captive dolphins (Caldwell & Caldwell 1965, 1968, 1979; Caldwell et al., 1990), which field work with wild dolphins helped to affirm (Herzing, 1996; dos Santos et al., 1995; Sayigh, Tyack, Wells, & Scott, 1990; Sayigh, Tyack, Wells, Scott, & Irvine, 1995, Sayigh et al., 1998; Smolker & Pepper, 1999). Simultaneously, studies continued in captivity (Burdin, Reznik, Skornyakov, & Chupakov, 1975; Janik & Slater, 1998; McCowan & Reiss, 1995a, 1995b, 2001; Miksis, Tyack, & Buck, 2002), and in the open sea (Cook, Sayigh, Blum, & Wells, 2004; Fripp et al., 2005; Watwood, Tyack, & Wells, 2004; Watwood, Owen, Tyack, & Wells, 2005). Some of the studies used temporarily restrained dolphins, which mixes both approaches, and provided critical test cases to specific functions (Esch et al., 2009; Janik, Sayigh, & Wells, 2006; Watwood et al., 2005). And additional data from captive studies further explored aspects that were difficult to identify in the wild

(Harley, 2008). We suggest that only the synthesis of both captive and wild dolphin studies yielded the current stage of knowledge about signature whistle functions, and that this example should be replicated in the study of other important aspects of dolphin behavior as well.

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