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Overlap between Information Gained from Complementary and Comparative Studies of Captive and Wild Dolphins

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Dolphin behavior has been observed in both captive and wild settings for years. Comparisons of captive and wild aquatic mammals have proven difficult because of limitations placed on observers in both arenas; still research conducted in each setting provides details often unavailable from the other environment. For example, internal body states (e.g., hormone levels) that might effect the expression of certain behaviors cannot readily be measured from wild dolphins; however, they can be routinely documented during husbandry behaviors. Conversely, detailed documentation of dolphin travel patterns is more readily available from long-term studies of wild dolphins; and while travel patterns are not applicable for study from captive individuals, observation of movement patterns within a pool can be examined to provide insight into an individual's behavior or inter-individual interactions. Long-term observations from three captive and three wild dolphins study populations are presented comparatively to illustrate how work on groups in each setting can complement one another. Additionally, data from a survey of trainers (50 surveys distributed with 17 completed surveys received) suggests that dolphin trainers interpreted several behaviors in ways that were consistent with observations of wild dolphins. For example, tail slapping was reported mainly as irritation (45.5%) or frustration (22.7%), but was also suggested to occur in play (31.8%). Pectoral fin rubs were used in appeasement (15.4%), comfort (7.7%), and affection (26.9%) more so than in sexual (7.7%) contexts or not at all (7.7%). Jaw claps, hitting, biting, chasing and ramming were observed in aggressive contexts in both captivity and the wild. More significantly, there were no consistent differences between wild and captive dolphins reported by surveyed trainers. The author's ongoing research program merges advantages from both environments to facilitate a more thorough understanding of dolphin communication and society.

Dolphin behavior has been observed and documented in both captive and wild settings for years (Defran & Pryor, 1980; Dudzinski, 1998; Herman, 1980; Saayman, Taylor, & Bower, 1973; Townsend, 1914). Comparisons of captive and wild aquatic mammals have proven difficult because of limitations placed on

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observers in both arenas (e.g., focus on anatomy, physiology and husbandry care or murky water and low tolerance to boats or swimmers, respectively). During the past 20 years, observations of wild dolphins have encompassed more detail from the underwater perspective (Dudzinski, 1998; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Dudzinski et al., 2003; Herzing, 1993, 1997; Sakai, 2003; Kogi, Hishii, Imamura, Iwatani, & Dudzinsk, 2004). At the same time, captive facilities have become more likely to include underwater viewing ports. These factors, coupled with improved technology for documenting underwater activity, provide an avenue for a more detailed examination and comparison of dolphin behavior from both wild and captive locations.

More than 35 species of cetacean have been maintained in artificial environments since the early 1860's (Defran & Pryor, 1980). While descriptions of specific behaviors were first provided by Townsend (1914), the majority of information collected on captive dolphins has focused on collection, transport, husbandry and medicine (Defran & Pryor, 1980). As a result, information on species-typical or comparative behaviors of captive cetaceans is relatively rare (Caldwell, Caldwell, & Siebanaler, 1965; Saayman et al., 1973). Recent behavioral studies of wild dolphins have been weighted largely towards free-ranging individuals and groups: usually, observations are confined to surface follows or documentation of general behavioral activities (Sjare & Smith, 1986; Weilgart & Whitehead, 1990; Würsig & Würsig, 1980). Recently, exceptions to research confined to surface observations are available; for example, studies that make use of active acoustics (manmade sonars) to track movements of animals underwater (Benoit-Bird & Au, 2009).

Systematic behavioral observations of captive dolphin social groups provide valuable information on specific events among associates as related to age/sex classes, group dynamics, or individual interactions. Conversely, few, if any, systematic or quantifiable data gathered from field studies of dolphin social behavior have been used for understanding the behavior and interactions of captive delphinids. Notable exceptions include Vergara and Barrett-Lennard (2008) in her research studying the contact calls of belugas (*Delphinaptera leucas*) with respect to their identification, usage and ontogeny and a comparative study of pectoral fin contact between individual dolphin pairs from three study populations—two wild and one captive (Dudzinski, Gregg, Paulos, & Kuczaj, 2010). Comparisons of data collected on a social group of captive dolphins with data collected on free-ranging individuals would elucidate details of dolphin associations, behavioral interactions and social life. Observations of dolphins in artificial environments can yield lengthy, detailed records of interactions among individuals within a group. Records also provide physiological and reproductive histories that might affect certain behaviors. Data from wild groups provide information on the behaviors, social relationships, individual association patterns and groupings of dolphins in their natural setting.

A comparative study of individual associations, specific behaviors and social groups observed in both captive and free-ranging dolphins will provide a better understanding of delphinid activity as related to both environments.

Information concerning group dynamics and individual roles within different group types would result from such an investigation, as would clues for the development of programs for environmental enhancement within captive settings. Conversely, observations and sampling from captive dolphins might link physiological or hormonal changes with behavioral actions. Both observational and physiological data collected in the study of captive dolphins can inform our understanding of both external (e.g., conspecifics, trainers, objects in the environment) and internal (e.g., hormonal state, health) motivators or factors that might affect the external expression of behavior. Few studies have yet to examine behaviors and behavioral exchanges between dolphins in association with information from blood draws or other physiological parameters. Data gained from such paired studies would facilitate better-informed management and conservation decisions and practices. Comparing the behavior of captive and wild dolphins has the potential to provide details related to assessing the welfare of both groups by increasing the sample size of behavioral observations both diurnally and seasonally (Veasey, Waran, & Young, 1996). That is, a wealth of data at varying times of day covering all four seasons is possible to be collected from captive individuals. The bulk of effort in studying wild dolphins is often related to simply locating the individuals and groups; this effort is mute when studying captive individuals thus facilitating a greater emphasis on observations of the individuals during their activity as opposed to looking for groups.

The focus of this paper is to present details of the author's extensive observations on captive and wild dolphins from several locations to inform a discussion of how data from both settings can be mutually beneficial to research on dolphin behavior. In support of this topic, results and discussion from a previously unpublished survey that queried professional animal trainers about the behavior of dolphins in their care is included. The surveys presented to trainers asked them to respond to various questions about the behaviors they might have observed and to compare their observations to video depicting three species of wild dolphins from the underwater perspective. I will show that there is extensive overlap in the information that is gained from complimentary and comparative studies of both captive and wild dolphin behavior. This paper presents a summary compilation and discussion of how observations and research on both groups of dolphin can benefit each other.

Method

Three species of dolphin, from both captive and wild settings, were the focus of data collected from 1991 to 2009 (Table 1). Data collection protocols were consistent between study sites. Underwater dolphin behaviors were videotaped using a mobile video/acoustic system (MVA, Dudzinski, Clark, & Würsig, 1995). Focal animal follows were used to record dolphin behavior (Altmann, 1974; Mann, 1999). Selection of focal individuals or groups was based on dolphin proximity to the recorder and was determined after the researcher entered the water. Dolphins at both captive and wild study sites are habituated to human swimmers.

Table 1
Details per study site for long-term, longitudinal observations conducted by the author of both captive and wild dolphin groups.

Study Site	Species	Captive/wild	Years of Study	Resulting papers
White Sand Ridge, The Bahamas	*Stenella frontalis*	wild	1991-1995, 1997, 2000-2002	Dudzinski, 1996; Dudzinski 1998; Dudzinski et al., 2009; Dudzinski et al., 2010; Paulos et al., 2008
Bimini, The Bahamas	*Stenella frontalis, Tursiops truncatus*	wild	2001 – present (ongoing)	Dudzinski et al., 2010; Melillo, 2008 Melillo et al., 2009
Mikura Island, Japan	*Tursiops aduncus*	wild	1995, 1997 – 2007 (ongoing collaboration)	Dudzinski et al., 2003; Dudzinski et al., 2009; Dudzinski et al., 2010; Gregg et al., 2007; Gregg et al., 2008; Kogi et al., 2004; Paulos et al., 2008
Roatan Institute for Marine Sciences, Roatan, Honduras	*Tursiops truncatus*	captive	2003 – present (ongoing)	Dudzinski et al., 2010; Dudzinski et al., in prep
Dolphin Encounters, Nassau, The Bahamas	*Tursiops truncatus*	captive	2006 – present (ongoing)	Beard, 2007; Beard et al., in review; Dudzinski et al., in prep
Kolmårdens Djurpark, Kolmårdens, Sweden	*Tursiops truncatus*	captive	1994*	Dudzinski, unpublished data, 1994

*Data collected on the dolphins at the Kolmårdens Djurpark were conducted over a one month period in 1994 but represent the introduction for the author to captive animal studies and provided the author with insights to desensitization of the dolphins to the observer and some interesting dolphin practice behaviors. Thus, these observations are included in this paper.

Wild study populations & sites

Since 1992, the author or graduate students with the Dolphin Communication Project (DCP) have studied three groups of wild dolphins: two from the Bahamas and one from around Mikura Island, Japan.

White Sand Ridge, The Bahamas. This group of Atlantic spotted dolphins (*Stenella frontalis*) is a wild population found along the White Sand Ridge of the Little Bahamas Bank, which is ~64.5 km north of West End, Grand Bahamas Island. This area ranges from 6 – 10 m in depth with a white sandy bottom, and generally good visibility to at least 30 m. The data used in this study were collected in 1993 and 1994 and were from a longitudinal study on dolphin communication (Dudzinski, 1996, 1998; unpublished data); data were collected each summer from May to September. Boat trips were seven days long with five to six days spent at anchor and on-effort observations conducted from 07:00 h to 19:00 h while at anchor. During the years included, the identified population consisted of approximately 125 individuals with an overall equal female to male ratio (Dudzinski, 1996).

Bimini, The Bahamas. Since 2001, a group of wild Atlantic spotted dolphins (*Stenella frontalis*) known to associate with humans since the mid-1990s has been observed around Bimini, The Bahamas. Dolphins were searched for and observed from boat-based ecotour trips within 16 km of the coastline of North Bimini Island. Water depth was generally less than 20 m. Data were collected during each summer season from May to September annually, and opportunistically in other months. The spotted dolphin population around Bimini consists of approximately 90 identified spotted dolphins with a roughly equal 2:1 sex ratio (female:male), However, the sex is unknown for about one third of the identified individuals. Sex of individual dolphins was determined by inspection of the genital area; age class was determined using a combination of coloration patterns and relative size [described previously for pan-tropical spotted dolphins (Perrin, 1970), and Atlantic spotted dolphins (Dudzinski 1996; Herzing, 1997)].

***Mikura Island, Japan*.** This Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) group is a population resident to the area within 300 m of Mikura Island, Japan (Kogi, Hishii, Imamura, Eiji, & Dudzinski, 2004). Water depth at this location varied from 4 to 20 m. The seafloor was rocky and visibility was poor (generally less than 15 m) in comparison to The Bahamas. The identified population consisted of approximately 165 dolphins with an overall equal sex ratio (Kogi et al., 2004). Observations and data were collected from 1997 – 2007 by the author and her graduate students during a long-term, longitudinal study to understand signal exchange between dolphins. Data were collected during 88 boat trips from 1997-1999 primarily between May and September, though about ten trips were conducted between October and April from 1997 – 1998. From 2000 – 2007, data were collected during 2 to 3 hr boat trips between May and August each year.

Captive study populations & sites

The author or graduate students associated with the Dolphin Communication Project have observed captive dolphins from three facilities for ranges of eight days to seven weeks per visit to each facility from 1994 to 2009. These facilities and the study populations at each location are described below.

***Roatan Institute for Marine Sciences, Anthony's Cay Resort, Honduras*.** The dolphins of the Roatan Institute for Marine Sciences (RIMS) at Anthony's Cay reside near Bailey's Cay in water that ranges from beach to about 8 m depth. These dolphins have been video-recorded and observed since October 2002 in visits conducted once or twice a year. Data are collected during 30 or 60 min observation sessions daily or twice daily (as facility schedule permits) during each visit. The sex of each dolphin is known; ages are estimated by the RIMS team for wild-caught individuals and known for dolphins born at the facility. The population size for this group of dolphins has ranged from 17 to 24 during annual observations and has an age and sex distribution similar to that observed for the wild dolphin study groups included in this discussion.

***Dolphin Encounters, Nassau, The Bahamas*.** Dolphin Encounters (DE) encompasses more than three acres of surface area, with water depths up to 8 meters. Dolphins at DE have been video-recorded since May 2006, with two trips (averaging 10 days in length) annually in 2006, 2007 and 2008, and one trip in 2009 spent documenting dolphin behavior. Data are collected during 20 or 30 min observation sessions twice to three times daily (as facility schedule permits) during each visit. The sex of each dolphin is known; ages are estimated by DE for wild-caught individuals and known for dolphins born at DE. The population size for this group of dolphins has ranged from 17 to 20

during annual observations and an age and sex distribution similar to that observed for the wild dolphin study groups discussed herein was observed.

Kolmårdens Djurpark, Kolmårdens, Sweden. In 1994, the author spent four weeks observing two subgroups of bottlenose dolphins (*Tursiops truncatus*) in the Delfinarium at the Kolmårdens Djurpark, Kolmårdens, Sweden. One subgroup of 5 individuals (1 adult male, 2 adult females, 2 juvenile females) was in the main pool (Delfinarium: 50 m x 20 m x 4 m and 3500 m^3) and another subgroup of 3 dolphins (3 adult females) was in the newly completed lagoon pool (approx 25 x 30 m, 6 m deep and 2000 m^3). Both of the large pools were connected by a middle holding pool (13x13, 3.5 m deep and 500 m^3). The author observed the dolphins non-invasively and did not interact, touch or feed any of the dolphins. General behavioral observations were conducted in advance of acoustic data collection on the accuracy of the mobile video/acoustic system (Dudzinski et al., 1995). That is, a stationary hydrophone array was created and used simultaneously with the mobile video/acoustic system to confirm the latter's accuracy in sound-source localization. Fifteen underwater observation sessions were conducted ranging from 5 to 15 min per session (the 5 min session was truncated because of dolphin tactile curiosity directed at the author).

Trainer survey methods

Over two years (2001 – 2003), with the goal of refining hypotheses to develop a systematic comparative study of both captive and wild dolphin behavior and communication, a summary video that depicted various wild dolphin behaviors (individual and interactive) was compiled and paired with two accompanying surveys with the aim of querying trainers about the behavior of "their" dolphins as compared to those depicted on the videotape. More than 50 video copies and surveys were distributed to participants at two international conferences (30th EAAM Symposium and 30th IMATA Meeting) that dolphin trainers regularly attend. Surveys were directed towards trainers, though copies were available to any interested person involved with dolphins in captive collections (e.g., veterinarians, behaviorists).

The summary video was 25-minutes representing the behavior of three dolphin species recorded underwater in three geographic locations: Atlantic spotted dolphins (*Stenella frontalis*) - Bahamas, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) – Mikura Island, Japan, and dusky dolphins (*Lagenorhynchus obscurus*) – Patagonia, Argentina. All video records were gathered during studies of dolphin behavior and communication inclusive from 1992 to 2001 (Dudzinski, unpublished video data; see also Dudzinski, 1998; Gregg, Dudzinski, & Smith, 2007; Paulos, Dudzinski, & Kuczaj, 2008; Dudzinski et al., 2009, 2010). With graduate students in the Psychology Department of the University of Southern Mississippi, two surveys were developed, one brief and one detailed. (Surveys available on request from the author.) Trainers were sent both surveys to complete: the brief survey requested information about the trainer and the facility while the detailed survey focused specifically about the dolphins in their care – their behavior, vocalizations and other activity. The aim was to objectively query trainers regarding the behavior they would watch on the video in comparison to the behavior they routinely witnessed from dolphins in their care. As such, the surveys and video were developed specifically with dolphin trainers in mind. A four-page summary of background information related to each species and details related to study length and topic(s) was also included. Copies of the brief and detailed surveys are available from the author.

Trainer survey behavior list. Our goal was to have trainers compare the images on screen from the video with their experiences and observations of the animals in their care. When distributing the video and surveys, a detailed list of behaviors (i.e., the behaviors used to identify the actions on video for our studies) of the different video segments was not included so that participants could view and score the videos without our bias for behavior description. The list of behaviors was created based on how dolphin actions are defined from research focused on the wild dolphins, which was given to participants via mail after the majority of completed surveys had been received. Generally, the behaviors provided to respondents include actions involving interaction with calves and juveniles (e.g., "babysitting," infant or echelon swim positioning, nursing), tactile contact (e.g., body or pectoral fin rubbing, touch) various swimming (e.g., circle swims, bell-to-belly swims) or approach behaviors (e.g., head on, oblique) that might or might not include vocalizations (e.g., buzzes, clicks or whistles), mimicry of other dolphins or swimmers, synchronous actions, aggressive or agonistic

behaviors (e.g., biting, hitting, ramming) and sexual actions. (A detailed list of the behaviors provided is available from the author.)

Results

Effort and observations of each study group

White Sand Ridge, The Bahamas. Data were collected with a mobile video/acoustic system (Dudzinski et al., 1995) from 1992 – 1995, 1997, and 2000 – 2002, with a total of 2,316 hrs of effort (time searching for dolphins) and 47 hrs of video data recorded. These data were collected as part of a long-term, longitudinal study of intra-specific communication among dolphins (Dudzinski, 1996, 1998; Dudzinski et al., 2009; Paulos, 2004; Paulos et al., 2008).

Bimini, The Bahamas. From 2003 – 2008, a total of 586 days were spent in the field and 286 boat trips were conducted, yielding almost 1,233 hrs of effort. On 250 of the 286 boat trips (87.41%), at least one dolphin sighting was included, with dolphins in view for 22.16% of total effort time. On 194 boat trips (67.83%), at least one underwater encounter was conducted; 6.44% of total effort time was spent observing dolphins under water. When underwater video is recorded, dolphins are in view approximately 50% of the time. These data were collected as part of a long-term, longitudinal study of intra-specific communication among dolphins (Melillo, 2008; Melillo, Dudzinski, & Cornick, 2009).

Mikura Island, Japan. Video with stereo audio data were collected consistently from 1997 to 2008 during 3 to 4 hour boat trips from either Miyake Island or Mikura Island to observe the dolphins around the latter island. The distance between Miyake and Mikura is 18 km and Miyake boats were roughly 15 m long; the trip between the islands took roughly 45 min and 2 to 2.5 hrs were spent within 300 m of Mikura on each boat trip. A total of 575 hrs of effort were spent searching for dolphins from which 92.5 hrs of video data were recorded. These data were collected as part of a long-term, longitudinal study of intra-specific communication among dolphins (Dudzinski et al., 2003, 2009; Gregg, Dudzinski, & Smith, 2007, 2008; Kogi et al., 2004; Paulos, 2004; Paulos et al., 2008).

Roatan Institute for Marine Sciences, Anthony's Cay Resort, Honduras. Data collection was conducted during visits to the facility ranging in length from one week to seven weeks. Underwater observations were either 30 or 60 min sessions with continuous video recording. One to three sessions were conducted daily during each visit. Because these dolphins were captive (both wild-caught and captive-born), no effort is expended to locate dolphins. A total of 86 hrs of video were collected: 30 in 2003, 14 in 2004, 8 in 2005, 11 in 2006, 8 in 2007, 4 in 2008 and 11 in 2009. These data are included in the long-term, longitudinal comparative study of dolphin communication (Dudzinski, unpublished data, 2003 – 2009; Dudzinski et al., 2010).

Dolphin Encounters, Blue Lagoon Island, The Bahamas. The author began data collection on the group of dolphins resident to Dolphin Encounters in 2006 with one to two visits per year and data collected in 20 to 30 min sessions.

One to three sessions were conducted daily during each visit. Because these dolphins were captive (both wild-caught and captive-born), no effort is expended to locate dolphins. A total of 45 hrs of video were collected: 15 in 2006, 12 in 2007, 15 in 2008 and 3 in 2009. These data are included in the long-term, longitudinal comparative study of dolphin communication (Dudzinski, unpublished data, 2006 – 2009; Beard et al., in review).

Kolmårdens Djurpark, Kolmårdens, Sweden. Two to three observation sessions, each 15 to 30 min in duration, of the dolphins in the main pool were conducted to document general behavior patterns and habituate the dolphins to the author's presence. The goal was to desensitize the dolphins to the author such that they would ignore the author as observer whether on the platform or in the water. Fifteen trials of 5 to 15 min duration were conducted with the mobile video/acoustic system and the stationary hydrophone array, beginning after the 10th day of observations. For all but one underwater session, the dolphins mostly ignored the observer while in the water and on the platform; during one truncated session (5 min duration), the two youngest dolphins expressed much inquisitive behavior toward the observer including pushing the observer with their rostrums. Thus, the session was aborted and the observer exited the water. Still, the author spent more than 12 hours at Kolmårdens Djurpark observing dolphin behavior from the surface while collecting ~5 hrs of underwater video and audio data. These data serve to inform the complimentary and comparative information that can be gleaned when one studies dolphins from both the captive and wild settings.

As a side note related to the small amount of data collected at Kolmårdens Djurpark, the observations that I made at this facility were the catalyst that ignited my quest to study and document the behavior and vocalizations of both captive and wild dolphins. These observations formed the beginning foundation for my focus of delphinid behavior and communication from the underwater vantage point. Thus, their inclusion, even at a sample size much lower than for the other field sites.

Trainer survey responses

From 50 distributed surveys and videos, 17 responses (34% return) were received completed: 10 from facilities and trainers in Europe, two from Japan, one from Mexico, and four from the USA. The majority of the facilities replied regarding *Tursiops truncatus*, the species housed at each facility that participated in the surveys. A few respondents made observations or remarks about other species; however, the focus for this survey was small delphinds, specifically *Tursiops* sp. or *Stenella frontalis*.

Responses related to captive dolphins and facilities. Dolphin group size at facilities of the respondents ranged from 2 – 23 dolphins (mean = 7 dolphins, median = 5). Overall, group dynamics (e.g., group size, age and sex composition) were similar to the average and median group sizes and characters documented for both wild Atlantic spotted and bottlenose dolphin study groups (Brunnick, 2000; Dudzinski, 1996; Kogi et al., 2004).

The number of pools ranged from one to nine pools available to dolphins. The majority of trainers reported that dolphins have the ability to self-separate from peers based on the shape and number of pools available to the dolphins. Whether the dolphins had the ability to self-separate was a question that was asked to determine how closely the setting of each facility mirrored that encountered for wild dolphins included in the 25-minute video. Twenty of the 30 pools included in responses possess underwater viewing ports. Of the pools with underwater viewing, 25% (n = 5) allow total viewing access of the underwater space occupied by the dolphins; 75% (n = 15) allow partial viewing into the pool(s). How trainers use the underwater viewing ports relative to training schedules and shows varied considerably among respondents: 10% (n = 2) always used the ports, 45% (n = 9) sometimes used them, 30% (n = 6) rarely used the ports, and 15% (n = 3) never used the underwater viewing ports for training or during shows. These ports likely represent an untapped potential for use by trainers and researchers interested in behavioral studies of dolphins.

Because data on wild dolphins used to create the 25-minute video were gathered while swimming with dolphins, we queried trainers regarding in-water training sessions and their interactions or contact with dolphins. While the majority of trainers used in-water interactions during working sessions (always 37.5%, sometimes 43.8%) and public demonstrations (always 53.8%, sometimes 38.5%), it is not consistently used between facilities (Fig. 1). Similarly, training might occur during in-water sessions, but free-swims with dolphins are only sometimes (42.9%) to rarely (35.7%) to never (14.3%) included. Still, dolphins are tactile with their caregivers, often soliciting touch in the water 87% of the time during the few existing free swims (Fig. 1). Dolphins regularly solicit touch from trainers at the side of each pool as well.

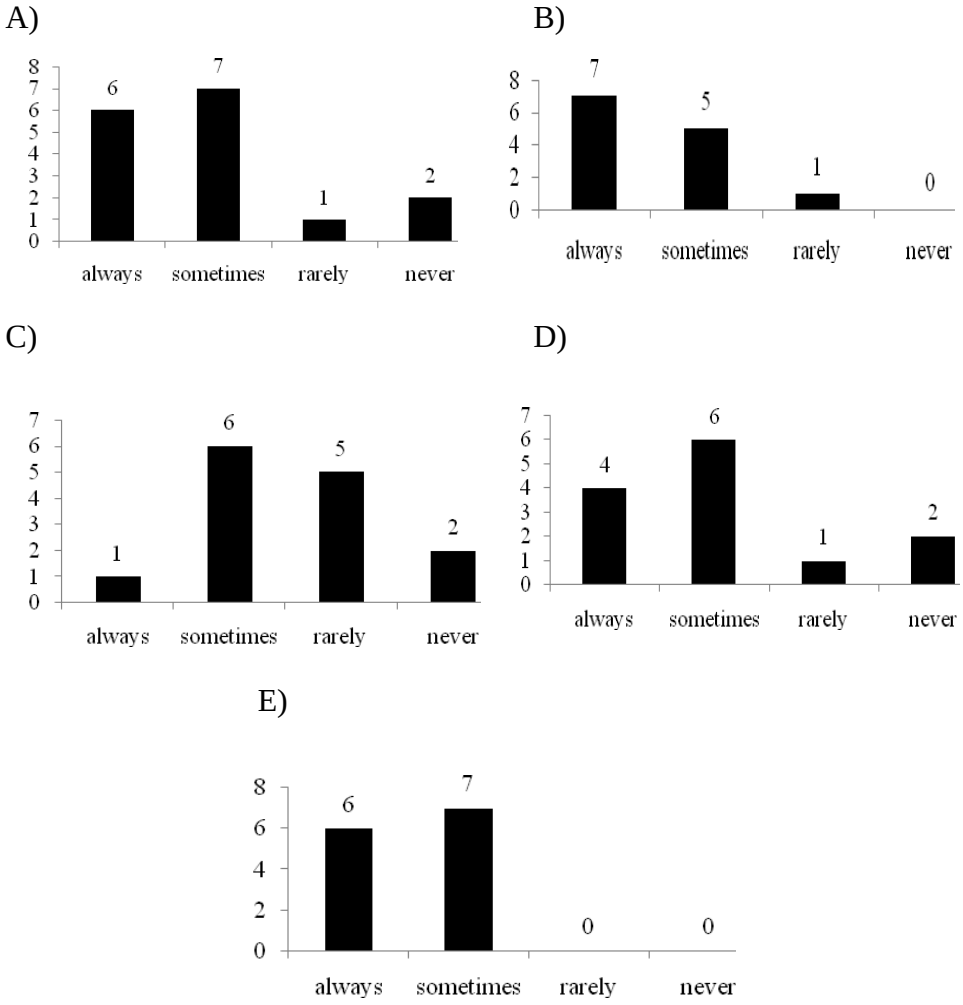

Figure 1. A) Does In-Water Training Occur with, B) Does In-Water Training Occur with Public Demos with, C) Do Trainers have Free-Swims with, D) Is Tactile Contact from Trainers solicited by, and E) Is Pool-side Tactile Contact Solicited by Dolphins. Y-axis indicates frequency of occurrence, and sample sizes provided above each bar.

Because dolphins play with each other and a variety of objects in the wild, questions were asked about toys that dolphins might have available for play. Trainers reported that dolphins frequently (always 33.3% and sometimes 60%) had toys of a wide variety available to them (Fig. 2). Toys were made available to dolphins at different times in a 24 hr period depending on show schedules, social make-up of the group, and facility type (Fig. 2). Free time (48%) comprised the majority of time when dolphins had toys available, although toys were present during training sessions (20%) as well (Fig. 2).

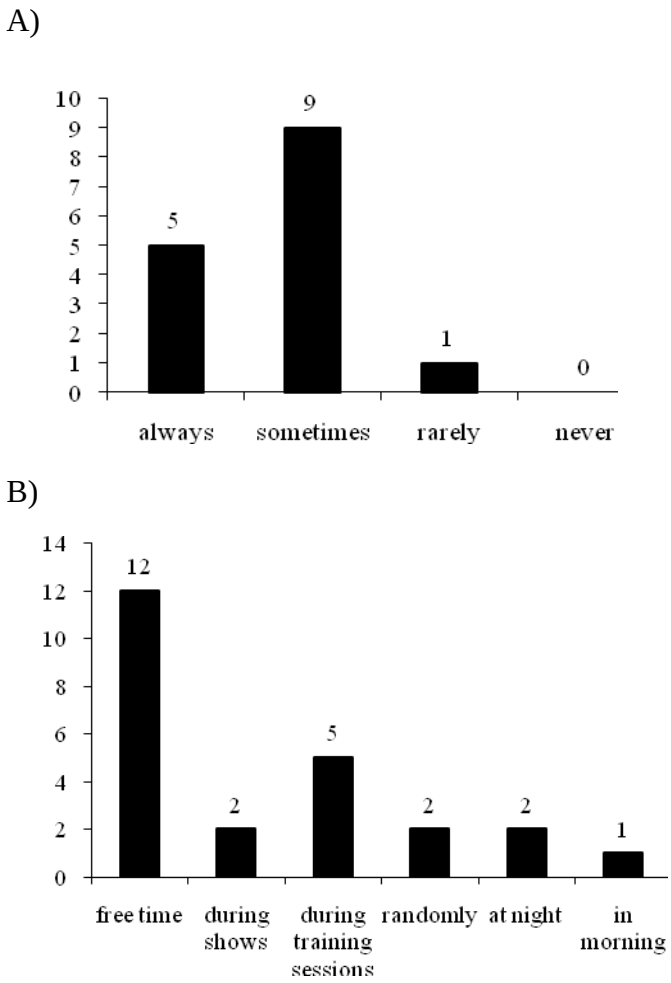

Figure 2. Dolphin Toys. A) How often and B) when are they available to dolphins. Y-axis indicates frequency of occurrence, and sample sizes provided above each bar.

Comparison between video-documented and captive dolphin behavior. In general, trainers reported more behavioral similarities than differences between dolphins shown on the supplied video with those in their care. In fact, four trainers wrote that they "saw no differences between the video and their dolphins." Two other respondents replied that "everything they saw on the video, they have seen among their dolphins."

A few specific questions regarding readily identifiable, specific behaviors were included to query trainers on possible function(s) of these behaviors (Fig. 3). These behaviors were to determine whether trainer respondents and researchers (who developed the surveys) agreed about potential functions of selected behaviors from video and direct observation. Trainers reported that tail slaps were a sign of irritation (n = 12, 71%) or an alert call (n = 12, 71% to group members, but that

they were also sometimes used to display frustration (n = 7, 41%) or during play (n = 7, 41%, percents do not total to 100 because multiple functions were reported by trainers). These replies agree with our observations of tail slap function(s) and of those reported in the literature (Defran & Pryor, 1980; Östman, 1994).

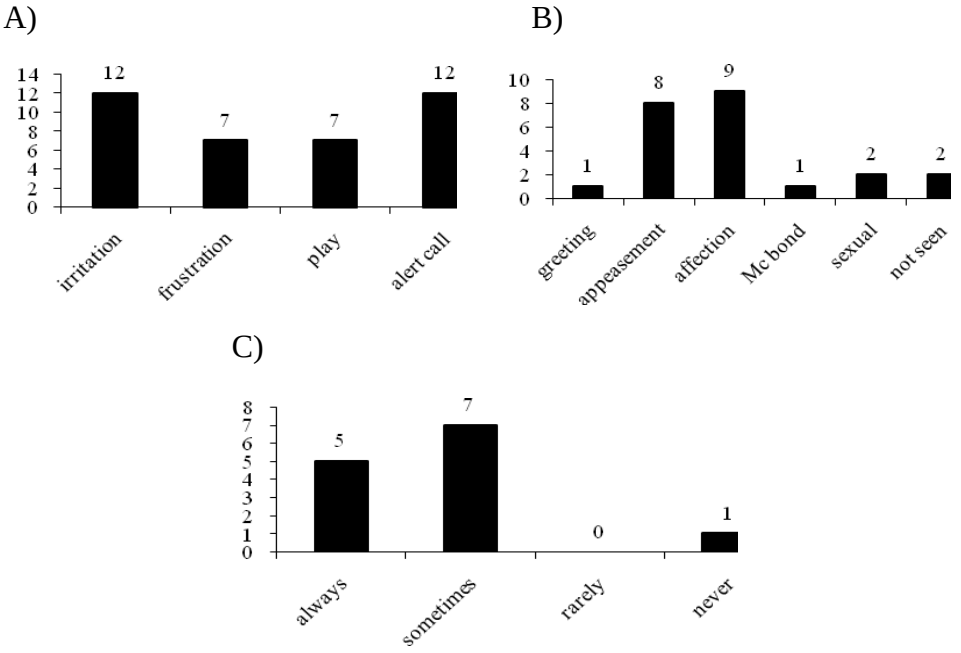

Figure 3. A) Tail slapping, B) pectoral fin rubs, and C) dolphin vocal behaviors – what do they mean? Y-axis indicates frequency of occurrence, and sample sizes provided above each bar.

Pectoral fin rubs and touches have recently been examined in detail in two wild dolphin study groups: Bahamas' Atlantic spotted dolphins and bottlenose dolphins at Mikura Island (Dudzinski et al., 2003, 2009; Sakai, 2003). In both groups, dolphins were observed to exchange pectoral fin contact for social and hygienic functions. In fact, contact with the pectoral fin varied minimally between sexes and age classes and between species from both locations (Dudzinski et al., 2009). Trainers reported dolphins using pectoral fin contact primarily as a method of appeasement on an agitated peer or as affection (Fig. 3).

All trainers reported observations on sexual behavior similar to that presented on the video; responses were descriptive in nature and not in response to a specific query regarding sexual behavior. Behaviors listed by trainers included erections, penile penetration of the blowhole and genital area of females or other males, and males and females using their pectoral fin or fluke tips to penetrate another dolphin's genital slit.

On the survey, questions about aggressive behaviors were included. Trainers reported that the following behaviors possessed an aggressive intent: jaw claps, hitting, biting, ramming, chasing, tail slapping, s-postures, raking, crowding,

face-offs, pectoral fin slaps, chuffing and gate fighting. Replies indicated these behaviors were aggressive and not likely to be observed in play between individuals, which contradicted somewhat with observations of play from among wild dolphins during which younger individuals might use actions typically defined as aggressive – maybe for practice.

Discussion

Comparative studies of the behavior and communication of captive and wild dolphins can be complimentary and provide a more complete and comprehensive understanding of both individual and group behavior. More than 20 years of observations on dolphins in both settings have informed the author's view with respect to conducting research on animals in both venues (Beard, 2007; Beard et al., in review*;*Dudzinski, 1996, 1998; Dudzinski et al., 2003, 2009; Gregg et al., 2007, 2008; Kogi et al., 2004; Melillo et al., 2009; Paulos et al., 2008). Additionally, a survey of marine animal trainers confirmed that both researchers and animal care professionals can use information and results from wild animals to inform enrichment and assessment of animal behavior for individuals in the captive arena: categorization and qualification of behaviors was essentially the same for researchers observing wild dolphin behavior from under water as for trainers who work with dolphins every day.

Overall, trainers reported significantly more similarities in behavior between wild and captive dolphins than differences. Two respondents stated that all the behaviors were the same between the video and "their" dolphins while two also indicated no differences observed. A few behaviors were specified with functional meaning queried to assess reliability between our interpretations with those of the trainers: agreement was high (~ 95%). Thus, trainers appeared to have reviewed the video-documented behavior of the wild dolphins with the same assumptions that researchers followed when analyzing the raw video data. For example, trainers and researchers were in agreement regarding the function of tail slaps: tail slaps by dolphins often occur dozens of times in succession, create loud, low-frequency underwater and air-borne sounds, and usually convey threat or frustration (Pryor, 1990).

Pectoral fin contact

Pectoral fin contact between conspecifics can have both hygienic and social functions (Dudzinski et al., 2009; Sakai, 2003). Where on the body contact occurs can also signal potential function for this tactile behavior. Dolphins soliciting pectoral fin contact with their rostrum or belly might be requested contact for hygienic reasons (e.g., to scratch an itch) while those touching the lateral peduncle of a peer could be asking for future assistance in a fight (Dudzinski et al., 2009). Trainers' response for pectoral fin contact function contradicted slightly with what was routinely observed for pectoral fin contact among wild dolphins, who seemed to use pectoral fin to pectoral fin contact as a

greeting behavior but still used pectoral fin to body contact for appeasement or to solicit a specific response from a peer (Dudzinski et al., 2010). From the survey, only one trainer reported pectoral fin rubs as a greeting. Observations of the bottlenose dolphins at DE and RIMS suggest that pectoral fin to pectoral fin contact is not primarily used as a greeting but more generally in tactile exchanges (Dudzinski et al., 2010). Pectoral fin responses might include reciprocal rubbing or partnering with the initiator in a scuffle against others.

Dolphins in the wild might routinely be separated in time or space from conspecifics for significant duration. Because the fission-fusion society of dolphins is heightened in the free-ranging situation, with larger and smaller groups of dolphins merging and splitting depending on activity and group composition, it is likely that pectoral fin exchanges are important for greetings. Dolphins in captive collections live within a more fixed, overall group composition, and are thus less likely to rely on regular greeting behaviors. It would be interesting to observe each dolphin sub-group during reunion after a separation (for veterinary or other reasons) to see whether greeting behaviors might be used and whether they are similar to those identified among wild dolphins or if their actions might be modified to reflect their environment.

In the wild and in captivity, dolphins often use their bodies, pectoral fins and dorsal fin to rub the bodies, pectoral fins, dorsal fin and flukes of peers. Dolphins will swim belly-to-belly or be aggressive with one another in courtship behaviors or with mating (Johnson & Norris, 1986; Norris, Würsig, Wells, & Würsig, 1994). Dolphins are tactile animals and are often seen in close proximity or touching peers as they travel, rest or socialize. The results from our preliminary comparative examination of captive and wild dolphin behavior suggest that touch is exchanged similarly in both settings. A more thorough study of dolphin actions, especially tactile exchanges, between both environments is likely to elucidate more subtle differences.

Play versus aggression

Because most dolphinaria/aquaria do not have groups of only young dolphins (five or more juveniles), it was expected that few trainers would reply that aggressive actions might also be observed during play or slightly escalated social activity. Play behavior has been characterized as a time for young animals to learn the meaning and function of certain behaviors (Fagen, 1981). Young animals must learn how and when to use proper social signals and play activities afford them the opportunity to practice for adulthood (Bekoff, 1984). In my observations of wild dolphins, juveniles and calves are often witnessed practicing or playing among themselves with aggressive actions (e.g., biting, chasing, underwater tail hits, posturing, etc.). Even when young dolphins use aggressive behaviors with adults, the latter's response is typically not an act of aggression. Young dolphins in captivity have been observed experimenting with a variety of behaviors and toys (Kuczaj & Highfill, 2005; Kuczaj & Makecha, 2008; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006), though trainers might not always have an opportunity to

witness these actions in the course of their day. That is, when a trainer is near a pool or with the dolphins, the animals are usually focused on the trainer and the related activity. Researchers who do not interact with a group of captive dolphins are often given the chance to witness behaviors not displayed in a trainer's presence, such as a young dolphin teasing and playing with several adults (personal observation at Kolmårdens Djurpark, 1994). Thus, gathering observations both in and out of a trainer's presence is important for obtaining a representative, random sample of dolphin behaviors at any facility.

Captive dolphins are provided access to a variety of toy types with which they play, including balls (footballs, round balls, small basket balls), hoses (with or without running water), hoops (hula and other), rings, floats of various size and shape (fenders, dice, noodles, foam mats), water jets, surfboards, buoys, ropes with floats attached, PVC tubes with food, ice, brushes, man-made algae, frisbees, windsurfing sail, fish, and other elements from the natural environment. Both wild and captive dolphins have been observed and reported to play with sea lions, sharks, and people to varying degrees. Facilities with natural enclosures might present fewer artificial toys because dolphins play more with objects that already exist in their habitat (e.g., live fish). In the wild, dolphins play with seaweed, fish, octopi, sea cucumbers, birds, sand, rocks, shells, people, and more (see for instance "medusa tossing" in dos Santos & Lacerda, 1987).

During my observations of both wild and captive dolphins, juveniles express more inquisitive actions and play behavior. This is not to say that adults do not engage in play, indeed they do more so than other social mammals (Fagen, 1981). However, juvenile dolphins – both captive and wild – will show more interest in human swimmer and in the researcher and camera system (personal observation). Individuals from both environments will poke with their rostrums at swimmer fins and at the camera. Avoiding eye contact, physical contact or participating in play will alert the dolphins to the fact that the research observer will not interact (personal observation, discussions with dolphin trainers). That is, after a few observation sessions of either wild or captive dolphins, it is possible to habituate the dolphins to the camera and observer's presence: in short, "this human is different and won't play" is communicated. While anthropomorphic in expression in this paper, it is possible to observe the natural behavior of dolphins given a period of annual habituation to the same human researcher.

General behavioral observations

At times, observations of wild dolphin behavior are made which defy immediate explanation and having a reference to a particular behavior documented from captive dolphins, even if presented in anecdotal format helps provide a better understanding of the function of some actions more swiftly than having details from one population alone. For instance, in the mid-1990s, a subadult female Atlantic spotted dolphin from the Bahamas was observed to "faint": she stopped swimming at the surface and sank to the seafloor without moving her body. She landed on the sandy seafloor, rested for about 10 seconds and then back to the

surface. This behavior was also documented from a subadult female Indo-Pacific bottlenose dolphin around Mikura Island, Japan, in 2001. A plausible explanation for this action came from a veterinarian working in Italy who was treating a female subadult bottlenose dolphin for a broken jaw; halfway through the first week of treatment, the female fainted (exact behavior described above). The trainers were concerned and raised her to the surface, took blood. Blood parameters were normal, except for a slightly elevated progesterone level (C. Gilli, Aquaria di Genova, Italy, personal communication, 1996). It was postulated that her actions were "behavioral" and not physiological: there were two adult males on the other side of netting while she was being treated. Similarly, the wild females were in social groups of mixed sex. Observations from both captive and wild settings suggest that subadult females might "faint" when sexually receptive to get the attention of a male dolphin. This is information that would likely have taken decades to obtain from observations of wild dolphins alone.

All animals use both subtle and overt cues when assessing, and subsequently interacting with, the environment around them, including the actions of other individuals whether friend, foe or prey. Dusky dolphins in Argentina systematically search an area looking for fish: they leap in a specific fashion and swim abreast of conspecifics (Würsig & Würsig, 1980). According to the Würsigs, while leaping it seems that dusky dolphins also cue on flocks of birds that might be indicative of a large school of fish just below. The birds represent a cue to the duskies in the same way that a trainer could represent feeding time to a captive dolphin. In fact, several trainers reported that dolphins often stationed or waited at poolside prior to a training session or feeding time. Thus, wild and captive dolphins appear to learn from the regularities in their environment, which has implications for training and environmental enrichment for captive animals (Lacinak, Turner, & Kuczaj, 1996; Kuczaj & Xitco, 2002).

Limitations of the Presented Studies

There are two major limitations that could impeded functional comparisons of data collected from both captive and wild dolphin study groups: 1) a substantial difference in effort expended as related to the amount of video data collected, and 2) confirmed agreement of behavioral interpretations based on similar backgrounds and knowledge or at least mutually reviewed historical information.

Captive dolphin groups are readily available to observe from both above and below the water surface. Coordination with facility managers and trainers to conduct observations around a commercial swim program or the husbandry routine set for care and feeding of the dolphins is facilitated by open and consistent communication between researchers and the facility staff. Communication with the staff confirms agreement in mutual or overlapping interpretation of various documented behaviors from the dolphins and provides details on each dolphin's suite of behaviors and current health. These details are important when a researcher's goal is to examine potential internal motivators (e.g., reproductive

state) to the expressed and documented behaviors exchanged between individuals. Understanding the background knowledge of all trainers at a facility serves to confirm that behaviors are being considered from shared viewpoints between trainers and researchers.

Wild dolphins often require significantly more effort to collect video data for reliable and consistent examination of their behavioral exchanges. When studying wild dolphins, the researchers must first locate a sub-group or few individuals. Once found, the group activity and behavior is assessed before underwater observations can be made. For our wild dolphin study sites, the range in return of effort expended is between 1% and 19%. In the Bahamas, where dolphins can be found near shore to 40 miles from shore, effort has been 1% (White Sand Ridge) to 10% (Bimini), while around Mikura Island, effort ranges from 15-19% with dolphins typically encountered within 300 m of the shore. Our average return on effort for the captive study groups is 80-85%. As clarification when referring to return on effort, for every 100 minutes of observation time, the percent values relate to the number of minutes of video recorded.

Even though a much larger amount of video data are collected during a shorter period of time spent observing the captive dolphin groups, our team has spent several months per annum observing and documenting the wild dolphins such that the amount of data available per site for comparison is typically quite similar. Additionally, all data are collected following the same protocols; thus, direct comparison between datasets is facilitated.

Conclusions

Within the past two decades, several dolphinaria worldwide have begun to house dolphins together in larger pools; a trend that is also apparent in zoos and wild animal parks (Gorman, 1994; Inglis & Shepherd, 1990). This restructuring of facilities and captive populations is a dedicated effort to create breeding groups and to enhance the quality of life of the animals while providing more options to manipulate the dolphins' social setting. Well-adjusted, healthy dolphins are important to a successful breeding program; and providing an atmosphere that is behaviorally and socially stimulating, as well as physically large enough (note: to date there has been no documented evidence supporting a relationship between reproductive success and pool size), will increase the likelihood of a successful breeding program. Comparable data sets including both captive and wild populations will provide insight in the application of observational data on the social systems of free-ranging dolphins to management and enhancement programs in captive settings.

By sharing our perspective and observations on wild dolphin behavior with those individuals who work closely with captive dolphins (i.e., trainers, veterinarians), we gain insight into what can be learned by comparing the behavior of dolphins from both settings. The captive arena allows for consistent lengthy, detailed surface and underwater observations both diurnally and seasonally. In addition, hormonal and other physiological parameters can be assessed regularly

from captive dolphins and possibly linked with behaviors as having causal relations or as indicators of general health. A more thorough comparative and complimentary examination of dolphins from both environments is warranted. The response and assistance from trainers to the surveys helped refine questions and procedures applied when conducting a more comprehensive study of captive and wild dolphin behavior – specifically looking at the functions of pectoral fin contact between individuals (Dudzinski et al., 2010). Future studies that expand upon information gleaned from simultaneous surface and underwater observations, while adding more extensive directional audio recording (with arrays) and playback experiments will facilitate a more complete understanding of dolphin communication and behavior. Merging data collected on dolphin behavior with husbandry records of dolphin health – physiological health – and association patterns will inform research regarding potential internal and external motivating factors that could affect the expression of some behaviors. Using overlapping and complimentary comparative data on dolphin behavior from both wild and captive settings will provide a thorough understanding of dolphin society and communication.

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