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International Journal of Comparative Psychology

Title

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Permalink

<https://escholarship.org/uc/item/1m99p540>

Journal

International Journal of Comparative Psychology, 32(0)

ISSN

0889-3667

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Publication Date

2019

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Methodological Considerations for Comparison of Cross-species Use of Tactile Contact

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Cross-species comparisons are benefited by compatible datasets; conclusions related to phylogenetic comparisons, questions on convergent and divergent evolution, or homologs versus analogs can only be made when the behaviors being measured are comparable. A direct comparison of the social function of physical contact across two disparate taxa is possible only if data collection and analysis methodologies are analogous. We identify and discuss the parameters, assumptions, and measurement schemes applicable to multiple taxa and species that facilitate cross-species comparisons. To illustrate our proposed guidelines for evaluating the role played by tactile contact in social behavior across disparate taxa, this paper presents data on mother-offspring relationships in the two species studied by the authors: chimpanzees (*Pan troglodytes schweinfurthii*) and dolphins (bottlenose and spotted, *Tursiops truncatus* and *Stenella frontalis*, respectively). Cross-species comparative studies allow for a more comprehensive assessment of the similarities and differences with respect to how animals traverse the relationships that form their social groups and societies.

Keywords: dolphin, chimpanzee, tactile contact, touch, cross-species comparisons, mother-offspring interaction

Comparative psychology has a long history of establishing methodology, questions, and evolutionary explanations for just about any construct imaginable (see review by Gariépy, 1998). However, like the legendary phoenix, the influence of this field continuously ebbs and flows, often requiring re-emergence from ashes to once again establish its importance in the vast field of psychology (Abramson, 2015). Time and again, special issues point out the cross-cutting influence of comparative psychology (Abramson & Hill, 2018; Miller & Hill, 2014) in topics such as clinical psychology (special issue prepared by Marston, 2017, categorization (special issue prepared by Plowright, 2017), or cognition (Zentall, 2018). One commonality across these articles is the need to create methodologies that facilitate cross-species comparisons (e.g., Byosiére, Chouinard, Howell, & Bennett, 2017; Eaton et al., 2018; Hill, Dietrich, Cadena, Raymond, & Cheves, 2018; Smith, Watzek, & Brosnan, 2018; Zentall, 2018). As identified in many of the papers referenced above, methodologies tend to be biased toward the species currently being tested, especially if apparatus or experimental stimuli are involved (i.e., can the species see color, use a limb to touch or pick up something, or respond to stimuli positioned at certain distances or heights given the lateralized or binocular position of their eyes). Similarly, if phylogenetic comparisons, questions on convergent and divergent evolution, or homologs versus analogs are of interest, the behaviors being measured must be comparable (i.e., collected with similar methodology and assumptions) before conclusions and generalizations can be made.

The special issue on physical contact or touch, for which the current paper was written, emphasizes the importance of continuing to study the role of physical contact in terms of either experiencing contact from another stimulus or initiating contact toward another stimulus. Involving the entire body, unlike the other sensory systems that target specific modalities and body parts, the receptors for somatosensory information are

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‡ This paper was part of the Special Issue on Touch published in 2018.

specialized for a variety of sensory experiences (sharp contact vs. soft contact, deep stimulation vs. surface stimulation, greater sensitivity vs. less sensitivity) that function to encourage survival (reviewed by Montagu, 1978; McGlone, Wessberg, & Olausson, 2014). In humans, research has continued to explore the haptic sensory system with an increasing number of special issues devoted to this topic over the years (e.g., Thayer, 1986a, b; Lederman & Klatzky, 2007; McGlone & Spence, 2010). Although tactile contact appears to function (i.e., learn about an environment, promote social development and interactions) similarly across many different mammals (cows, e.g., Duve & Jensen, 2011; elephants, e.g., Bates et al., 2008; primates, e.g., De Waal & van Roosmalen, 1979; Dunbar, 2010; Harlow, 1958), the roles of convergent or divergent evolution have not been fully explored (e.g., Dunbar, 2010; McGlone et al., 2014).

In the last few decades, the role of physical contact has been examined in terms of physiological responses and social relationships for many human and nonhuman animals (reviewed by McGlone et al., 2014). In premature human infants, “kangaroo care” (i.e., skin-to-skin contact between the infant and an adult, reviewed by Engler et al., 2002) and infant massage (Field, 2014; Field, Diego, & Hernandez-Reif, 2010) have been linked to faster physical development of premature systems, such as weight gain, gastro-intestinal development, lung development, brain development (e.g., Feldman & Eidelman, 2003), thermoregulation (e.g., Ludington-Hoe, Anderson, Swinth, Thompson, & Hadeed, 2004), self-regulation of sleep and attention (e.g., Feldman, Weller, Sirota, & Eidelman, 2002), and synchrony in respiration and heartbeat (e.g., Ludington-Hoe et al., 2004). This intervention was influenced by the marsupials themselves and developed by the Hospital Materno Infantil in Bogotá, Colombia, in response to limited resources at the hospital (Programa Ambulatorio de Prematuros [Ambulatory Program for Premature Infants], Anderson, Marks, & Wahlberg, 1986). Similarly, a line of research with rats (*Rattus ratta*) has demonstrated that human handling of rats altered neurochemical and neuroendocrine processes and neural anatomy (e.g., Meaney, Aitken, Bhatnagar, & Sapolsky, 1991; Meaney, Aitken, Van Berkel, Bhatnagar, & Sapolsky, 1988). As reviewed recently by McGlone et al. (2014), social relationships in many species are mediated by different types of tactile contact, eliciting many positive effects for young and old (i.e., autonomic responses, including heart rate, respiration, affective responses, and cognitive processing efficiency). Clearly, the power of “touch” is evident, and yet we still have so much to learn about its effects on humans and nonhuman animals.

Socially, physical contact can be used to communicate information, such as stopping an action, continuing to perform an action, indicating the presence of a conspecific, or expressing a particular affective state. Physical contact can also be used to develop and maintain relationships or to mitigate a current affective state or situation (e.g., grooming and consolation practices in nonhuman primates, De Waal & van Roosmalen, 1979; investigative trunk behaviors in elephants, Slade-Cain, Rasmussen, & Schulte, 2008; hugs or embraces in humans, Jones, 1994). The extant research in many nonhuman animals tends to be filled with descriptive research in which types of contact are identified, quantified, and categorized into social contexts (e.g., Bates et al., 2008; De Waal & van Roosmalen, 1979; Dunbar, 2010; Duve & Jensen, 2011; Harlow, 1958; McGlone et al., 2014; Palagi et al., 2016). Some strides have been made to examine the functionality of physical contact during social interactions. Research on licking of neonatal pups by rat mothers (Davis et al., 2017) and rough and tumble play in rats (Pellis, Himmler, Himmler, & Pellis, 2018) have suggested that, like Harlow’s (1958) findings with rhesus monkeys, depriving rats of either of these opportunities leads to degradation in social and cognitive development, altered neurobiology, and future survival and reproductive success. Dudzinski and colleagues have attempted to examine the behavioral function of specific types of contact between dolphins, namely pectoral fin contact between dolphins (Dudzinski, 1998; Dudzinski et al., 2012; Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Paulos, Dudzinski, & Kuczaj, 2008), rather than more mechanistic functions (e.g., neurobiological functions). Testing a number of possible hypotheses, Dudzinski and her colleagues concluded that pectoral fin contact was used to mediate existing relationships in

both natural and managed care settings for bottlenose dolphins, *Tursiops* spp. and Atlantic spotted dolphins, *Stenella frontalis* (Dudzinski et al., 2012; Dudzinski et al., 2010; Dudzinski & Ribic, 2017). These conclusions supported earlier observations of contact between wild Indo-Pacific bottlenose dolphins (*T. aduncus*, Sakai, Hishii, Takeda, & Kohshima, 2006a) and contact by captive dolphins following aggressive bouts (Tamaki, Morisaka, & Taki, 2006) in which subsequent pectoral fin contact appeared to function as a reconciliation tool, much like grooming in primates (Hemelrijk, & Ek, 1991). Another type of contact called “contact swimming” occurs when two animals (typically adult females, which is unusual) swim side-by-side with static, continuous contact between a pectoral fin and the body for extended periods (Connor, Mann, & Watson-Capps, 2006). Connor et al. (2006) speculated that this unusual contact between females may have been an attempt to reduce stress or aid the female’s swimming during consortships by the males during breeding.

To directly compare the social function of tactile contact across species, it is critical then that the methodologies be analogous. The purpose of this paper is to provide a guideline to facilitate cross-species comparisons by establishing the parameters, assumptions, and measurement schemes that can be applied to multiple taxa and species. Despite posing more questions than answers, this paper and proposed guidelines should provide a framework for future research. If we share our ideas, we can enrich each other’s data and the research questions asked and promote our understanding of this phenomenon. To illustrate the proposed guidelines for evaluating the role played by tactile contact in social behavior, this paper will focus on mother-offspring relationships in the two species studied by the authors: chimpanzees (*Pan troglodytes schweinfurthii*) and dolphins (bottlenose and spotted, *Tursiops truncatus* and *Stenella frontalis*, respectively).

Chimpanzees and dolphins have been compared to each other frequently in a variety of behavioral and cultural studies (Bearzi & Stanford, 2007; Boesch, 2012; Connor, Mann, Tyack, & Whitehead, 1998; Connor & Vollmer, 2009; Pearson, 2011). As evidence has accumulated, a number of characteristics have emerged as being shared between these two disparate taxonomic groups: social systems, communication signals, dispersed foraging strategies, tool-use during foraging, sexual coercion, maternal care, behavioral milestones, socioemotional responses and behaviors, and a variety of cognitive abilities (reviewed in Bearzi & Stanford, 2007). Having similar types of fission-fusion social systems in which social groups are fluid and ebb and flow between small and large groups, as well as similar types of ecological pressures despite living in two, very different environments (aquatic vs. terrestrial), these two taxa continue to be standards for each other. Given the long periods of dependence and high levels of sociability for both taxa, the role of tactile contact in social interactions is one more measure to assess similarities and differences in the function of signal exchange and inter-individual interaction(s).

Social contact has been identified as one of the fundamental ways in which nonhuman primates maintain their relationships; examples of social contact include grooming in macaques (Majolo, Schino, & Aureli, 2012) and chimpanzees (Newton-Fisher & Lee, 2011), or embracing following aggressive encounters (Fraser & Aureli, 2008). The use of “contact” has also been a prevalent measurement of maternal behavior in non-human primates since the 1970s. Mother-infant interactions are measured typically by spatial proximity (Hinde, 1970). This measurement incorporates the frequency with which a mother-infant dyad is in contact and who is responsible for this contact (see, e.g., baboons, Altmann, 1980; monkeys, Hinde, 1984; vervet monkeys, Hauser & Fairbanks, 1988; Japanese monkeys, Schino et al., 1995; rhesus macaques, Berman & Kapsalis, 1999; Suomi, 1995, 1999; macaques, Fairbanks, 1996; bonnet and pigtail macaques, Weaver et al., 2004; Weaver & Waal, 2002, 2003; bonobos and chimpanzees, DeLathowres & Eslacker, 2004; chimpanzees, Pusey 1983, 1990). The emphasis in this approach is placed on describing who initiated the contact and who received it. This approach is very successful in showing how tactile contact is a variable that plays an important role in differentiating different mother-infant dyads.

Tactile contact has also been measured from a developmental perspective. Tomonaga and colleagues (2004) conducted a longitudinal study of three infant chimpanzees and reported that during the first two months of life all of the mother-infant pairs increased their engagement in mutual gaze, which corresponded with a decrease in cradling behavior by the mothers. A similar finding was reported from different captive chimpanzee populations (Bard et al., 2005).

Although contact has been incorporated in the past as a way of measuring social interaction (including mother and infant interaction) and given recent discoveries of the importance of tactile contact for the development of social interaction (Ackerley, Saar, McGlone, & Backlund Wasling, 2014; McGlone et al., 2014), it is necessary now to understand how this mode of interaction is used within dyads in a more detailed way. That is, a way that incorporates and describes how the different elements of tactile contact, such as quantity, duration, and quality (e.g., kinds of contact), play a role in social interaction.

Early studies of dolphin behavior and social interactions in both captivity and the wild described contact between individuals almost haphazardly. In mother-calf interactions, calf-initiated contact and mother-calf swim positions were described but not measured specifically (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss., 1999; Mann & Smuts, 1999; McBride & Kritzler, 1951; Reid, Mann, Weiner, & Hecker, 1995; Tavolga & Essapian, 1957). General affiliative and aggressive social interactions have been described with tactile contact mentioned but not measured specifically (e.g., Overstrom, 1983; Samuels & Gifford, 1997). Physical contact has been examined more closely in dolphins over the last 25 years with a particular focus on pectoral fin contact (see review of pectoral fin contact as defined in the literature in Sakai et al., 2006a).

In the mid-90s, Dudzinski began examining physical contact within dolphin dyads (Dudzinski, 1998), with her focus narrowing in the early 2000s specifically to pectoral fin contact between wild dolphins (Dudzinski et al., 2009). Her research initially identified the frequency, initiator, receiver, and body parts involved in contact. Using these variables, she compared several populations, finding only a few differences between different wild populations and no differences between wild and captive dolphin groups in the way any two dolphin dyads share pectoral fin contact (Dudzinski, Danager-Garcia, & Gregg, 2013; Dudzinski et al., 2010; Dudzinski et al., 2009). The latest research has indicated that pectoral fin contact appears to be used to establish and then maintain specific relationships between dolphins occurring most frequently between unrelated animals (Dudzinski & Ribic, 2017).

Research with wild Indo-Pacific dolphins (*Tursiops aduncus*) found not only that pectoral fin contact occurred fairly frequently between specific individuals, but also that it appeared to be lateralized such that almost half of the dolphins examined used their left flipper more frequently and for longer contact durations (Sakai, Hishii, Takeda, & Kohshima, 2006b). Contact swimming between females during consortships of males was noted because of its frequency and duration, which were unexpected for these adult females who were characterized as having weak associations as compared with the strong associations documented within male alliances (Connor et al., 2006). Although not examined specifically in these earlier studies, the findings of Sakai et al. (2006a) and Connor et al. (2006) support the Dudzinski and Ribic (2017) results that exchange of pectoral fin contact between nonkin male dolphins is a tool used for social bonding by some bottlenose dolphins.

It is clear from the literature (and our own observations) that individuals in dyads of both chimpanzees and dolphins frequently share a variety of forms of physical contact. Comparing tactile exchanges between

both taxa will offer insight into potential convergent evolutionary pathways for the role of tactile contact in the establishment, maintenance, and management of relationships within the societies of each species. Direct cross-species comparisons benefit when underlying research assumptions are analogous; in this paper, we provide an approach to conducting cross-species comparisons that facilitates a direct examination of potentially disparate datasets using, as an example, a comparative look at how mothers and their offspring share (initiate and receive) tactile contact with the forelimbs, hands, and pectoral fins.

Method

The aim of this paper is to provide an overview of the methodological considerations that are important for a cross-species comparison when using tactile contact as a mode of interaction. To examine these methodological considerations, we will use examples from a study currently being developed¹ that compares patterns of behavior exhibited by mothers and their offspring in dolphins and chimpanzees through the mode of touch.

Our studies of both species (i.e., dolphins and chimpanzees) used for this comparison rely on similar methodologies: we used focal follow protocols, collected video data, and randomly sampled individuals. For each species, the selection of a sample unit (focal individual) is based on chance with respect to which animals come into the observer's field of view. Still, effort was placed on collecting the same length of observation for each mother-infant pair.

Through our analysis, however, we discovered that the functional unit of comparison (see comment just below on tactile contact definitions) might not be exactly the same and that the actual data collected might not cover the same developmental periods for the offspring being studied (i.e., consider whether the developmental months are comparable between dolphins [precocial] and chimps [semi-precocial]). These subtle differences in underlying assumptions for data collected as well as interpretation of the behavioral exchanges within dolphin and chimpanzee dyads informed our broadening concerns as to whether all facets of each data subset were directly comparable. In this paper, our goal is to provide an overview that considers all the necessary variables that should be examined when making comparative conclusions to more completely illustrate the similarities and differences between social animal taxa. In particular, we will focus on the different ways in which the underlying assumptions and methodologies have to be consistent to allow for direct comparison of data on social interactions through the mode of touch.

To conduct cross-species comparisons, consistency in data collection, analysis, and the underlying assumptions is required. Because most cross-species comparisons are conducted on data collected on each species in advance of any consideration of a cross-species comparison, the data and underlying assumptions must be confirmed and clarified both after the fact (i.e., of data collected on each species) and a priori (i.e., prior to comparison analyses). One pertinent example from our comparison of dolphin and chimpanzee tactile contact is the understood definition of "tactile contact." For studies on dolphin tactile exchange(s), a distinction is often made between types of physical contact: static contact or touch and rubbing (i.e., active movement between a pectoral fin and another dolphin's body; e.g., Dudzinski et al., 2010; Dudzinski et al., 2009; Sakai et al., 2006a). In the primate literature, contact is the term used most frequently that can encompass static tactile contact or can describe active movement between a hand and body as when chimpanzees groom one another

¹ The aim of the ongoing research study referred to in this methods paper is to investigate whether mothers exchange tactile contact with their offspring similarly between these two taxa.

(Hemelrijk & Ek, 1991). From here on, we use the term contact to refer generally to physical/tactile contact shared by individuals within both chimpanzee and dolphin mother-offspring dyads; when referring specifically to static contact, we also use the term touch, whereas active movement between body parts will be referred to as rubbing. However, as it will be described in more detail below, it is important to take into account that while the definition and observation of a behavior can be readily developed and coded/observed, determining whether that behavior has the same function (or meaning) for both species is challenging. Researchers must attempt to identify, using characteristics of the tactile contact (e.g., static vs. moving, speed, etc.) and contextual clues, whether the basic unit of tactile contact is the same across species.

Methodologies Designed to Observe Contact Observation: Examples from Chimpanzees and Dolphins

The following is an overview of two methodologies used to observe contact in chimpanzees and dolphins. These will be used as case studies to illustrate how a direct comparison of the social function of physical contact across two disparate taxa is possible only if data collection and analyses methodologies are analogous.

Chimpanzees

Study subjects. Gombe National Park has three chimpanzee communities (subspecies *Pan troglodytes schweinfurthii*). The mother-infant pairs observed in this study belong to the largest of the three: the Kasekela community. The chimpanzees at the Kasekela community have been habituated and studied since the 1960s (Goodall, 1986). During the first phase of Botero's study, the first year of life of six infants was observed and videotaped. All infants had siblings and belonged to mothers with similar ranking (Murray, Eberly, & Pusey, 2006; Pusey, Williams, & Goodall, 1997). There was one difference among the individuals: Golden and Gaia were twins and had constant companionship with each other since birth. A detailed listing of the focal individuals and their family history is shown in Table 1.

Procedure. Interactions in mother and infant dyads were observed using videotape recordings (by Bill Wallauer from the Jane Goodall Institute [JGI]). These tapes have longitudinal information of different mother-infant pairs from 1993 to 2003, were part of the JGI research program, and provided a record of different families in the Kasekela community. We divided the first year of infant life into four categories: 0-3 months, 4-7 months, 8-11 months and 12 months (Table 1). We selected six mother-infant pairs based on the availability of footage for each pair. Second, we divided all available footage on each mother-infant pair into different behavioural contexts (BC); from video data and every 2 min, the mother and infant's behaviors were recorded as being in one of the following behavioral categories: aggression, breastfeeding, close contact, feeding, nesting, playing, grooming other subject, grooming infant, grooming self, reassurance, rest, travel, and weaning (Botero, MacDonald, Shanker, Pusey, & Wallauer, 2017a, 2017b), using focal sampling (Altmann, 1974).

Analyses of video tapes was completed with Noldus XT, a coding program that allows a detailed frame-by-frame observation of the interaction between mother and infant. In this phase of the study, the duration of contact given by the mother to the infant was the focus. This contact was termed *touch* and was defined as the mother making any movement that resulted in bodily contact with the infant, which was further subdivided into the following categories: touch with left arm, touch with right arm, touch with left leg, touch with right leg, and touch with head – this last category includes touching with head and/or mouth. Because the duration of these contacts was so short, data were reported in seconds. Ideally, the rate of contact would have been calculated by dividing the duration of maternal touch by the total observation time for the first year of the infant's life in each BC. Recording BC would allow us to document the rates of maternal touch during different behaviors for each mother-infant pair. We suggest this procedure as one of the ways in which touch can be recorded in mother-infant pairs, it would provide data on how touch is used in different contexts as the infant develops and matures. However, in this specific study, because the sample size is so small ($n = 6$), it was not possible to calculate such a detailed division. All rates of maternal touch during each BC in the infant's first year of life were averaged for each subject (Botero et al., 2017a, 2017b). We acknowledge that the decision to average touch for all BC for each chimpanzee pair separately is complicated because it raises developmental issues and maturity issues. It is possible that an average across age may not reflect how touch potentially varies developmentally and whether the function (or meaning) of touch could potentially change as an infant chimpanzee matures and develops.

As an example of the importance of development, a previous study (Botero, MacDonald, & Miller, 2013) found differences among the social and anxiety behaviors of these infants as adolescents, and, in studies currently in preparation (Botero et al., 2017a, 2017b), we expected to find a correlation between these social and anxiety behaviors and the kind of interaction patterns (i.e., frequency of touch) the chimps displayed with their mothers as infants. Future research that includes larger sample sizes could potentially remedy the need for a more graded developmental approach.

Table 1
Details of Both Study Groups – Chimpanzees and Dolphins – Discussed in this Paper

Chimpanzees			Dolphins		
Adult Female	Offspring	Sex/Age (mo) when data were collected	Adult Female	Offspring	Sex/Age (y) when data were collected
Fifi	Flirt	F (0-12 mo)	Alita	Fiona Anthony Cortez Lenca Dory	2, 3 + 1, 2, 3, + 1, 2, + 2, 3, + 1, 2
Fanni	Fudge	M (0-12 mo)	Carmella	Ritchie Ken Dixon Elli Stan	+ only 1, 2, 3, + 1, 2, 3, + 2, 3, + 1, 2
Gremlin	Golden	F (0-12 mo)	Cedena	Mika Bailey	3, + 1, 2, 3, +
Gremlin	Glitter	F (0-12 mo)		Pigeon Calli	1, 2, 3, + 2, 3, +
Sandi	Samson	M* (3-12mo)	Gracie	Maury Jack Luna Tilly Shawn	3, + 1, 2, 3, + 1 1, 3, + 1, 2
Pati	Titan	M* (3-12 mo)	Mrs. Beasley	Buster French Marg Vin	+ only 1, 2, 3, + 1, 2, 3, + 1, 2, 3, +

Note. For dolphins, listed years represent calf age(s) for which data were collected. For chimpanzees, four categories of ages were identified: 0-3 mo, 4-7 mo, 8-12 mo, and “+”. “+” in the dolphin sex/age column indicates dolphins observed older than 3 years of age. * For both Samson and Titan, data were not available for the period of 0-3 months as they were not observed.

Dolphins

Study subjects. A group of common bottlenose dolphins (*Tursiops truncatus*) reside at the Roatan Institute for Marine Sciences (RIMS; Anthony’s Key Resort, Roatan, Honduras). Dudzinski has been studying these captive dolphins at RIMS for more than 16 years (Dudzinski et al., 2009, 2010, 2012; Evans-Wilent & Dudzinski, 2013; Greene, Melillo-Sweeting, & Dudzinski, 2011). Roatan is 27 miles north of the Honduran coast and the dolphins reside around Bailey’s Key on the NW side of the island but inside the fringing reef system. The natural lagoon offers roughly 300 m² in surface area as a dolphin habitat with depths ranging from the shoreline to ~8 m. Over the years of data collection, the study population has ranged in size from 16 to 24 dolphins with a mixed age-sex (neonate to 30+ years old, both sexes) structure that is similar to the social dynamic documented for several wild dolphin groups (e.g., Connor et al., 2006; Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004). Individual dolphins were reliably recognized and identified based on scars, notches, rake marks, and pigment patterns on their bodies (e.g., Würsig & Jefferson, 1990; Würsig & Würsig, 1977).

Procedure. Data collected on pectoral fin contact exchanges between dolphins were part of a longitudinal examination of dolphin communication (i.e., behavior, acoustics, etc.) of several groups of dolphins studied by colleagues of the Dolphin Communication Project (e.g., Dudzinski, 1998; Dudzinski et al., 2009; Gregg, Dudzinski, & Smith, 2008; Melillo, Dudzinski, &

Cornick, 2009; Paulos et al., 2007). Underwater video with stereo, real-time audio (Dudzinski, Clark, & Würsig, 1995) was used to document dolphin behavior and sounds during interindividual interactions. Video data were limited by underwater visibility and sea conditions; observations were collected using a focal follow protocol and all-occurrence sampling (Altmann, 1974). Identified dolphins were opportunistically observed based on which dolphins were readily in view of the researcher underwater. Once the researcher was in position underwater, focal follows began when a (or several) dolphins were in view and continued until the dolphins left the camera's field of view.

Pectoral fin contact exchanges were event-sampled only from all videotaped data (for reliability and repetition) for all years of data (2003-2018) for all dolphin dyads. The focus of our comparative examination between chimpanzee and dolphin tactile contact includes only those pectoral fin contact exchanges between adult female dolphins and their calves. In addition to each pectoral fin contact event between one dolphin's pectoral fin and another dolphin's body, other data documented included date, "real" time of contact, and initiating and receiving dolphins (and their age and sex), as well as each dolphin's posture, contact duration, whether contact was static or a rub, and which individual ended the contact. We also documented the specific role that each initiator/receiver assumed: The rubber is the dolphin whose pectoral fin is involved in the contact, whereas the rubbee is the dolphin whose body is involved (Dudzinski et al., 2009).

Overlapping Considerations

Both taxonomic groups have been the subject of long-term longitudinal studies (16-57 years) into their social lives and societies. Both groups – the chimpanzees and the bottlenose dolphins – are habituated to the presence of humans in their environment either as research observers and/or as interactive participants (the dolphins participate in swim and encounter programs with human visitors). All data collection on both groups was video recorded using a focal follow sample protocol; documentation of tactile contact between individuals for both species used an event-sampling procedure (e.g., logging the number of tactile contacts between individuals as well as when and on what body part contact is made). Event samples of tactile contact within mother-infant dyads yielded results for review and analyses. For both taxa, observations were readily impacted by environmental conditions that could limit length of focal follows as well as affect the observers' ability to confirm physical contact occurred or even which individuals were sharing contact (even from video records). These considerations form the basis of the following paragraphs.

Similarities and Differences in Data Collection and Analyses

Data collection. Our research into dolphins and chimpanzees is based on long-term observational studies (Table 1, chimpanzees, JGI 57 years, tactile 11 years; dolphins: 15-25 years). This condition is ideal for observations of contact since it provides longitudinal data with respect to how this kind of interaction takes place across time. Longitudinal data also offer the potential opportunity to begin to tease out functionality of differing forms of contact. We do acknowledge, however, that there are differences in how longitudinal observations are conducted. For chimpanzees, touch is observed across months within a given year whereas for dolphins, contact was documented in shorter sessions over years. These disparate approaches to data collection for both species could impact the potential developmental differences we might identify for tactile contact, touch comparison between species, and the potential function(s) of those contacts between individuals.

Additionally, both of our studies follow noninvasive observation protocols – our goal is for our presence to impact the animals we observe as little as possible with the fervent hope that we are mostly ignored during data collection. For both taxa, focal animal sampling (Altmann, 1974) was employed: for chimpanzees, focal follows were often of long duration, ranging from 1-12 hr; for dolphins, the focal follows were considerably shorter in duration. That is, a dolphin became a focal for as long as the animal was in view, which

typically ranged from seconds to minutes but could be repeated throughout a 20- to 60-min session. An important similarity for data collection on both taxa is that no interaction was attempted with any study subject.

To examine contact in a functional way, focal follows are critical because of the potentially prolonged periods of observation. These prolonged periods of observation allow researchers to collect all information necessary, such as duration of contact or determining the body part(s) used and contacted, which in turn helps us understand the complexity of social interactions that occur through physical contact. Other methods, such as scan sampling, will not render enough information to collect these kinds of data. It is important to notice that if a researcher is interested in observing these types of detailed elements that factor into shared contact (e.g., the role duration might play in contact), then raw data must be collected as video. Use of video allows for repeated review of each captured exchange and interaction and for a detailed analysis of all qualitative elements of contact (e.g., kind of contact, part of the body used, etc.), as well as duration. Both of our studies include video data to allow for detailed analyses and replication as might be warranted. Chimpanzee data also included detailed field notes at the time of the focal sampling, though such was not the case for dolphins because the researcher was swimming with limited ability to write copious notes. Field notes were made by additional observers at the water surface after the researcher exited the water. Also, during review of videos, a data log of events and individually recognizable dolphins was created for every session. For both the chimpanzee and dolphin studies, the environment will often make it difficult to preserve field notes, though every effort must be expended to compile and retain details germane to collected data at the end of each day in the field. The reason why video sequences are important in these kinds of studies is that they provide a long-term archive of animal interactions while also allowing for reliability assessment and replicability in analyses.

One important difference that was found when comparing data collected on both species is the total length of observation. For chimpanzees, as indeed for most behavioral studies of terrestrial species, data are collected during extended periods of time where field seasons range from months to a year (or more) and where attention to season (i.e., rainy season and dry season) often determines the distribution of the observational periods. Meanwhile, for the dolphin study, data were collected during short research field sessions of 1-3 weeks in length, mostly during the same time of year annually or with two sessions per year in different seasons. Season was noted but does not seem to factor into our current understanding of within-dyad behavior exchanges, as compared with personality or relationships, for dolphins. Thus, differences in length of observational period and considerations of seasonal variation in each study of different species should be taken into account when addressing data collection assumptions in datasets, especially for comparative studies where season might impact one, if not multiple, study groups/species.

Finally, one of the prime directives in both studies was that the animals must ignore the observer when data are being collected. If the chimpanzees or dolphins did not ignore the researcher, then those data were not included in the resulting data set. When collecting data, it is important to pay attention to the animal's (s') behavior and potential curiosity of the researcher; for example, on rare occasions, if the dolphins showed too much inquisitiveness of the researcher, data collection would cease and the observer exited the water. For chimpanzee observations, it was also required for the observer to maintain at all times a distance of 12 m to the animals and to move away from a focal (for health reasons) if the animal(s) closed the distance to the researcher. For similar reasons, both of the current studies have observed human-habituated animals, which facilitates observations of naturally occurring, spontaneous behavior. To study tactile contact among individuals requires following individuals and documenting their interindividual interactions; however, if the animal subjects are too anxious because of human presence, it would not be possible to observe their social interactions.

Another requirement of this kind of study is the need for relatively good visibility. Visibility is critical when observing and measuring contact between individuals and small groups as they interact with each other. Underwater visibility in dolphin observations and the density of the vegetation in chimpanzee observations can limit what is recordable.

Data analyses. Field notes and video records should be coded in a consistent manner between studies to facilitate statistical analyses and assessments of the amount of data available for a comparison across species. From this information, each researcher can determine if behavioral frequencies, rates, or sequences will represent the core unit for review of contact allowing a cross-species comparison. Moreover, for cross-species comparisons, it is fundamental to consider the characteristics of contact (e.g., static contact, rubbing) that are going to be included in the observation and data analysis, as well as the way these characteristics might be operationalized. For example, determining how contact duration is measured (i.e., from what start point to end point) must be analogous between studies. Similarly, the type of the contact (e.g., static contact or active rubbing) must be identified without implying function; for example, rubbing behavior in dolphins has been likened to grooming in chimpanzees (e.g., Dudzinski et al., 2009; Hemelrijk & Ek, 1991), but without the requisite confirmation that the raw data are actually comparable so that function can be reliably assumed. Another important consideration is the body part involved in the contact exchange (i.e., for initiating and receiving contact); chimpanzees and dolphins have very different looking bodies, even though their forelimbs are homologues. Addressing anatomical similarities and differences in advance of comparing data sets is important to confirm so that potential confounding factors are mitigated.

Any researcher attempting a cross-species comparison for contact has to decide whether to include all forms of contact – static touches, rubs, short duration, long duration, etc. Another decision is whether all body parts used during contact should be pooled or examined separately. For this particular study, to observe dolphin pectoral fin contact exchanges, 11 body parts were identified to look at preference for body part. Dudzinski et al. (2009) and Dudzinski et al. (2010) found that the dolphins exhibited preferences related to initiator role as rubber or rubbee and body part and potentially to duration of contact overall when examining all dolphins, not only mother-calf dyads. These details are currently being compiled for the observed mother-calf interactions. Likewise, these differences have yet to be explored for chimpanzees. However, given the methodology of video analysis and the division of contact based on body parts (i.e., touch with left arm, touch with right arm, touch with left leg, touch with right leg, and touch with head), this analysis can be completed in the future; thus, highlighting the importance of video records for bringing datasets that might be considered disparate into a more compatible state for direct comparison. Preliminary findings from this chimpanzee dataset (Botero, personal observation, 2017) have shown that there may be a preference of body part used for contact depending on the age of the infant and the BC. For example, there is more use of contact by hand during travel than when feeding. This kind of analysis emphasizes even more the need for video analysis, as this medium of recording enables researchers to review contact at slower speeds and to examine each interaction in a complex way that includes, among others, contact duration as well as whether contact is a static touch or active rubbing. Moreover, it allows researchers an avenue to better understand potential social function(s) of specific actions by allowing them to observe the antecedent(s) of a tactile contact and associated behaviors, as well as potential consequence(s) or sequences that might follow.

Cross-species comparisons also require that within the observation of each species, researchers identify initiator and receiver. For dolphins, the roles of initiators and receivers have been observed and documented. For chimpanzees, when measuring mother and infant interactions, as it has been prevalent in most of the human primate literature (Montagu, 1978; Thayer, 1986a, b), only the contact initiated by the mother was recorded. However, as with the previous example, it is possible to use video analysis of raw data to

examine all contacts shared for dolphins and chimpanzees to allow for more direct comparison of contact between species. What is important, for the current purpose of this paper, is to emphasize the importance of asking in any future cross-species comparison whether it is important to focus on the maternal-initiated or offspring-initiated contact or both. Additionally, it is important to consider that current methodologies that emphasize the initiator and recipient of a tactile contact are a good starting point; however, incorporating more dynamic models where the interaction is considered communicative and bidirectional could provide more complex descriptions of the interaction. For example, a dynamic model approach might help determine the roles the initiator and recipient play in a communicative exchange based on their relationship history over time (for examples of more dynamic methodologies applied to humans, see Doiron & Stack, 2017; Mantis, Stack, Ng, Serbin, & Schwartzman, 2014).

While comparing data analysis procedures among species, it is necessary also to consider the numerous factors that contribute to making the data available for analysis. And, we have learned from a variety of studies that age, sex, developmental capabilities, and personality all factor into dyadic behavioral interactions within social animal groups (e.g., rhesus monkeys, Suomi, 2004, 2005). It was interesting to notice that in this particular case, for both dolphins and chimpanzees, maternal styles, individual differences in the mothers, and the behavior of the offspring play a role in the way contact takes place among different mother-offspring pairs.

Finally, it is also important to consider the individual characteristics of the species compared and the environments that surround them. For example, when comparing chimpanzees and dolphins, it is important to consider how the different ways in which each species moves is a characteristic related to how a contact behavior might be used. Consider, for example, the different ways in which chimpanzees engage in tactile contact while standing still and sitting down; that is, they place one hand on another chimpanzee's back while travelling together, and they sit down or stand in one place when engaging in grooming behavior. Dolphins are similar though they do not sit down per se and might simply slow their swimming speed rather than fully stopping. This difference in locomotion and body posture entails that when attempting to do cross-species comparison, we need to consider the different ways in which the species move in their environment (especially if comparing terrestrial and aquatic mammals).

Another crucial species difference that must be taken into account, especially for mother-offspring interaction, is their period of dependency and the age at which behavioral milestones are reached. For cross-species comparisons, it is important to consider which developmental months are comparable between dolphins (who are precocial) and chimps (who are semi-precocial) at birth through their first year. Is the first month of a dolphins' life equivalent to the first three months of a chimpanzee's life? When do they become similar developmentally? Or, does it really matter, if all that we are interested in is what types of maternal-initiated contact occurs along with offspring-initiated? Understanding these differences would allow us to compare how contact takes place between a mother and her offspring from a developmental perspective in different species that may have different developmental trajectories.

In summary, whether (1) cross-species comparisons focus on all forms of contact or only selected types of contact (only mother-initiated or mother- and offspring-initiated contacts), (2) the focus is on certain body parts or the whole body, or (3) those body parts are analogous or homologous, as long as these studies are consistent in how we approach data collection and analyses and as long as we confirm the underlying assumptions are compatible, we should be able to draw direct comparisons between data sets and species.

Discussion

Cross-species comparative studies allow for a more comprehensive assessment of the similarities and differences with respect to how animals traverse the relationships that form their social groups and societies. Confirmation that data sets to be contrasted share underlying assumptions is key for direct comparison of disparate species. Any data collected may have followed a certain protocol used to inform specific research questions that might not be particularly germane to a comparative examination; however, if the assumptions and potential confounding factors are known and compatible, then direct statistical comparison is often applicable. Similarly, analyses specific to one species or set of research questions do not require that the same approach be applied to a different species for a comparison, as long as the original “raw” data are available. Often when a cross-species comparison study is developed, a more detailed examination will require use of original, raw data rather than already-processed data points.

In our example comparing a primate with a delphinid, there were significant potential confounding factors, not the least of which included the anatomical and environmental differences between these taxa. Still, understanding the identified similarities and differences in tactile contact exchanged within mother-offspring dyads of both species will elucidate the evolutionary contexts and habitat interaction(s) that may have shaped the varying functional needs of physical contact between individuals. Comparing disparate taxa allows a broader perspective from which to understand the continuum along which signals lie for information sharing between individuals in all social species. Additionally, comparative research offers insight into each studied species as well as clarification of methods and analyses applied to the same. For example, it is important to consider what body parts are involved in contact interactions for each species and whether these parts have a function that is equivalent in different species (e.g., hand, pectoral fin). It is also important to consider the duration of contact; depending on the species and the environment (e.g., terrestrial, aquatic), movements may be slower or faster.

Previous research has found that tactile contact functions on many levels of communication (e.g., for disciplinary, instructional, calming, affection reasons, etc.) (see for example in human infants, Jean, Stack, & Fogel, 2009). In this paper, we found that in both species tactile contact is used in different contexts, which suggests that both species are using physical contact for different kinds of communication. By examining these different levels of communication, new questions will emerge and enable us to derive a more complete understanding of social life. For example, what are the differences in social lives of aquatic and terrestrial species, and how might the medium in which each species resides influence perceived similarities and differences? Or, what evolutionary links might exist between species or habitats or dyadic interactions that might have shaped the function of tactile contact? Approaching the topic of contact comparatively will hopefully build on the already existing foundations of contact in its role within development and social bonds. It is our goal that this paper within the context of the special issue will ignite others to study touch from a cross-disciplinary perspective.

Acknowledgements

This paper is a culmination of conversations among the co-authors as well as between the co-authors and several colleagues and students during the course of our research and educational programs. We thank these students and colleagues for their discourse. We thank the Jane Goodall Institute, the Dolphin Communication Project, the Roatan Institute for Marine Sciences, Sam Houston State University, and St. Mary's University for their support in association with each co-author's data collection and analyses, as well

as during the writing and preparation of this manuscript. This paper is contribution #119 from the Dolphin Communication Project.

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Financial conflict of interest: No stated conflicts.

Conflict of interest: No stated conflicts.

Submitted: September 7th, 2018

Resubmitted: January 13th, 2019

Accepted: February 3^d, 2019