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Effects of an Increase in Group Size on the Social Behavior of a Group of Rough-Toothed Dolphins (*Steno bredanensis*)

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Abstract

Little is known about the social structure of rough-toothed dolphins (*Steno bredanensis*), but general knowledge of dolphin social structure suggests that individual dolphins often engage in multiple social relationships. In the wild, rough-toothed dolphins often swim in tight subgroups, consistent with the notion that social bonds and proximity to others are important for this species. Such behavior may also facilitate physical contact, which has been demonstrated to play important roles in social interactions in other dolphin species. In this study, the social behavior of captive rough-toothed dolphins was examined before and after the unification of two separate animal groups (both subgroups, $n = 3$) to investigate the effects of an increase in group size and a change in social structure on social behavior. The strongest new social partnership was between two juvenile males. Prior to the merger of subgroups, one of the juvenile males spent more time with a juvenile female. This dyad maintained a high interaction rate; however, after the move, this male significantly increased interaction rates with another juvenile male. The results of this study demonstrate that the integration of two small social groups provided opportunities for new social relationships to form but did not affect stable social partnerships that already existed. The formation of new social partnerships appeared to be influenced by age and gender. Although these results are based on a captive population, they provide insight into social behaviors that may be relevant to understanding the dynamic social structure of dolphin societies in the wild as well as in captive settings.

Key Words: social behavior, tactile behavior, rough-toothed dolphins, *Steno bredanensis*

Introduction

Compared to many mammalian species, dolphins show a social complexity that is rivaled by only a few terrestrial species such as elephants and some primates (Norris & Dohl, 1980; Reiss et al., 1997; Connor et al., 1998; Connor, 2007). Like chimpanzees (*Pan troglodytes*, Strier, 2003), spider monkeys (*Ateles geoffroyi*, Ramos-Fernández, 2005), Serengeti lions (*Panthera leo*, Schaller, 1972), and sperm whales (*Physeter macrocephalus*, Whitehead et al., 1991; Connor et al., 1998), many dolphin species live in fission-fusion societies defined by fluid association patterns and changing group size. Fission-fusion societies are inherently complex because they represent a constantly dynamic social environment (Connor et al., 2000b; Marino, 2002) in which individuals move in and out of the group, often on a daily or hourly basis. Considerable social knowledge is required in order for group members to identify each other, recognize their position in the social hierarchy, form and maintain alliances, and engage in and interpret an extensive repertoire of social behaviors (Herman, 1991). Although group size and composition can vary depending on the species, location, food availability, predation risk, age, gender, and reproductive status of group members (Michaud, 2005), other factors can influence the formation of particular social groups. In two bat species (*Desmodus rotundus*, Wilkinson, 1985; *Nyctalus noctula*, Kozhurina, 1993), studies in captivity and in the field have shown that individual preferences among animals are responsible for the formation of long-term associations among colony members, indicating that, at least for some species, the interactions of certain individuals may be based on an individual animal's particular preferences for or against another animal.

Bottlenose dolphins (*Tursiops* sp.) sometimes form consistent long-term associations, generally between members of the same sex; for example, males will often form stable alliances with one or two other males in order to sequester and mate with receptive females (Connor et al., 1992, 2000a; Smolker et al., 1992; Waples & Gales, 2002; Wells, 2003). Adult females may also form stable associations within nursery groups, both with their calves and with other adult females in the group (Wells, 1991; Mann & Smuts, 1999; Mann et al., 2000). Because bottlenose dolphins live in fission-fusion societies, they likely have different levels of interaction based on individual associations and activities within each group type and size (Norris & Dohl, 1980; Norris & Schilt, 1988; Dudzinski, 1996). Associations among bottlenose dolphins are typically assessed via proximity, physical contact, and synchronous movement (Pryor, 1990; Connor et al., 2006).

Affiliative tactile contact may be particularly important for members of large delphinid groups that form smaller subgroups for foraging, resting, or traveling (Johnson & Norris, 1994). Tactile contact might facilitate or reinforce social bonds (since it is particularly common among closely bonded individuals) and might also re-acquaint individuals with other group members (Herzing, 1993; Mann & Smuts, 1999; Paulos et al., 2008). Physical contact occurs between dolphin mothers and their young, among groups of juveniles, and between males and females (Pryor, 1990). Connor et al. (2006) suggested that contact swimming (when one dolphin swims with its pectoral fin resting against another's lateral side) might communicate more specific information about the quality of the bond or serve as a form of stress reduction. Forms of tactile contact such as rubbing, petting, and grooming are commonly observed between closely bonded individuals in a variety of species, both terrestrial and aquatic (vervet monkeys [*Chlorocebus pygerythrus*], Seyfarth & Cheney, 1984; jackals [*Canis* sp.], Moehlman, 1987; other primates, de Waal, 1989; bottlenose dolphins, Herzing, 1993; Mann & Smuts, 1999; Dudzinski et al., 2010). Furthermore, contact might be used to promote rank in a social dominance hierarchy, reduce tension among group members, reduce the risk of parasitic infection, function in post-conflict reconciliation, and ward off potential predators or aggressive conspecifics of the touching individuals (Seyfarth & Cheney, 1984; Moehlman, 1987; Herzing, 1993; Dudzinski, 1996, 1998; Mann & Smuts, 1999; Paulos et al., 2008).

Although the social structure of rough-toothed dolphins remains largely unknown, some sources suggest that wild rough-toothed dolphins live in small groups (Addink & Smeenk, 2001; Pitman & Stinchcomb, 2002; Ritter, 2002; Kuczaj & Yeater, 2007). These groups have been observed swimming in synchrony and often swimming in such close proximity that they are in frequent tactile contact (Ritter, 2002). The existence of close associations and high occurrence of tactile behavior within the social group suggests that rough-toothed dolphins form strong social bonds (Ritter, 2002; Kuczaj & Yeater, 2007). Groups are commonly observed ranging between 10 to 20 individuals (Addink & Smeenk, 2001; Ritter, 2002) with studies indicating an average group size of 12 animals (Kuczaj & Yeater, 2007). However, groups might also be as large as 160 dolphins or as small as three individuals (Ritter, 2002). Such variability in group size allows for the potential development of multiple social relationships.

Among captive dolphins, the formation of a social hierarchy is especially apparent (Waples & Gales, 2002) and is often established and maintained by agonistic dominance relationships (Samuels & Gifford, 1997). As such, physical contact is not always affiliative, and behaviors such as biting (Norris, 1967; Parsons et al., 2003) and body slamming (Samuels & Gifford, 1997) are more likely aggressive in both captive and wild settings. However, it is important to consider the context in which these behaviors occur as oftentimes behaviors that are normally seen as aggressive can also be seen during play bouts (Dudzinski, 1996; Marten et al., 1996; McCowan et al., 2000). Since captive dolphins are restricted in the number of potential alliances they can establish, changes to their group structure could have a drastic effect on their social dynamic (Waples & Gales, 2002).

Captive facilities sometimes find it necessary to add or remove an animal from the social group (Burks et al., 2001). These animal movements are similar to a fission-fusion society in the wild, albeit involuntary in captivity. The death or removal of a close associate, change in the dominance hierarchy, or the introduction of a new individual are all likely to affect the social behavior of small groups more so than larger groups. Additionally, changes in social behavior may be more pronounced in captivity than in the wild (Burks et al., 2001). In a study of pigtail monkeys (*Macaca nemestrina*, Erwin & Erwin, 1976), an increase in group size resulted in an increased frequency of aggressive behaviors. Bercovitch & Lebrón (1991) also found that division of one large social group of rhesus macaques (*Mucaca mulatta*) into two smaller subgroups increased aggressive behavior.

David's (1987) score is a good measure of interaction success for which one individual is clearly dominant based on the outcome of the aggressive interaction (Gammell et al., 2003). Animals that usually dominate have high positive scores, and those that are usually dominated have large negative scores (Whitehead, 2009). Therefore, based on these indices, it could be predicted that within a dyad, the more dominant individual would more frequently be the actor than the reactor. Calculating David's score is especially useful in social groups that show reversals in the direction of dominance at times (Bang et al., 2010). Recent studies by Koren et al. (2008) and Jaeggi et al. (2010) have calculated social hierarchies in various mammal species using David's score to interpret interactions.

The present study took advantage of a unique opportunity to assess how the merger of two small social groups affected the social interactions of the individuals. Given that free-ranging rough-toothed dolphins are thought to have fission-fusion social organization (Addink & Smeenk, 2001; Pitman & Stinchcomb, 2002; Ritter, 2002; Kuczaj & Yeater, 2007), the unification of two separate groups of captive rough-toothed dolphins allowed for an examination of the manner in which the involuntary fusion of two groups affected social behavior.

Methods

Subjects

The study subjects, six rough-toothed dolphins that were stranded, rehabilitated, and deemed unreleasable by the National Marine Fisheries Service, were housed in two separate pools at Gulf World Marine Park in Panama City Beach, Florida. Two of the rough-toothed dolphins, Doris and Ivan, stranded together. The other four animals each stranded on separate occasions. The two pools were located on different sides of the oceanarium and were not in view of one another. Pool A was in-ground, and Pool B was above ground, with an additional viewing platform from above. At the beginning of the observation period, the six rough-toothed dolphins were divided equally into two groups (Table 1). On 14 September 2006, the animals were combined into a single pool in order to create a single, larger social group. These rough-toothed dolphins had never been in a larger social grouping since being in captivity. None of the rough-toothed dolphins (with the exception of Doris and Ivan who stranded together) had ever been exposed to the individuals in the other pool prior to the unification.

Table 1. Captive rough-toothed dolphins at Gulf World Marine Park

Dolphin	Sex	Age class at time of move
Pool A		
Vixen (V)	Female	Adult
Largo (L)	Female	Juvenile
Ivan (I)	Male	Juvenile
Pool B		
Astro (A)	Male	Juvenile
Doris (D)	Female	Adult
Noah (N)	Male	Adult

Data Collection

Observations were collected opportunistically from January 2006 through January 2007, with an emphasis on the month after the integration. Behavioral observations were made in 2-min intervals over 30-min periods to create ethograms, utilizing an instantaneous scan sample protocol for all six focal animals (Altmann, 1974). Prior to the combination of the two social groups, a total of 286 min of ethogram data were collected for both Pool A and Pool B combined. Following the fusion of the subgroups, a total of 375 min of ethogram data were collected.

Behavioral Analysis

To investigate social interactions among all the rough-toothed dolphins both pre-move and post-move, interaction rates were determined from the behavioral ethogram data using *SOCPROG* (Whitehead, 1999, 2008). For the analysis, the behaviors were divided into symmetric (behaviors with no clear initiator or receiver) and asymmetric (directional behaviors). Symmetric social behaviors included pair swim, social play, and group social ball (see Appendix 1 for specific behavioral definitions). A network analysis was also completed in *SOCPROG* for the symmetric social behaviors. For the network analysis, strength is the sum of interaction rates of any individual with all other individuals. An animal with a high strength indicates that this individual has a strong interaction rate with other individuals (Whitehead, 2009). Similarly, individuals with a high eigenvector centrality will have relatively strong interaction rates to other individuals with relatively high interaction rates. Eigenvector centrality is a measure not only of how well one individual is associated to another but also how well that other individual is associated with additional individuals. Lastly, an individual's affinity is a measure of the strength of its associates, weighted by the interaction rate between them. Individuals with a high affinity have relatively high interaction rates with individuals who have a high strength (Whitehead, 2009).

The asymmetric behavioral data were divided into four separate analyses: (1) nonsexual contact behavior, (2) sexual contact behavior, (3) chase behavior (due to difficulty deciphering context for all chases), and (4) aggressive behaviors (see Appendix 1 for categorization and definition of behaviors). In addition to the interaction rates, measures of asymmetry for each dyad were calculated using van Hooff & Wensing's (1987) directional consistency index. A chi-squared test for asymmetry and a dominance index (David's [1987] score) were also calculated using *SOCPROG* for all four sets of asymmetric data.

Results

Symmetric Social Interactions

Interaction rates were assessed for rough-toothed dolphins pre-move and post-move based on ethogram data. The distribution of interaction rates shows each individual's interaction rate with each of the other individuals. Interaction rates for symmetric social behaviors, including pair swim, social play, and group social ball, are shown in Table 2. There was a significant difference in the interaction rates pre-move (M = 7.64, SD = 3.52) and post-move (M = 1.98, SD = 0.52) for symmetric social behaviors: t(56) = 13.59, $p < 0.001$. The highest interaction rate (26) pre-move was between Ivan and Largo (Table 2A). The individuals with the highest interaction rate (52) post-move were also Ivan and Largo (Table 2B). Therefore, these two animals maintained their symmetric social behaviors as a consistent dyad even after the formation of the larger social group. A chi-square test of goodness of fit revealed that Ivan and Largo maintained a high rate of interaction and that there was a significant increase in interaction rate post-move: X^2 (1, N = 39) = 8.67, $p = 0.003$. In addition, there was also a high interaction rate (42) between Ivan and Astro, which was a newly developed interaction post-move.

A network analysis was also calculated using *SOCPROG* for the symmetric social behaviors both pre- and post-move. Table 3 shows the strength, eigenvector centrality, and affinity for each individual in the social "network." As shown in Table 3A, Ivan and Largo both have high strength and eigenvector centrality pre-move with each other in the same pool. This means they each tend to have strong interaction rates with other individuals (each other, in this case), and any additional social partners also have higher interaction rates. Additionally, Largo and Ivan have the highest affinity, which means they have more interactions with individuals who have high strength (strong interaction rates with others—each other in this case—before the larger social group was created). This social network changed after the formation of the larger social group. Overall, the animals in Pool A had a higher affinity pre-move. Ivan has the highest strength and eigenvector centrality (Table 3B). However, post-move, Astro demonstrated the highest affinity. This may be due to Ivan's switch from Largo to Astro in terms of a preferred social partner in symmetric social interactions. All of the individuals increased their strength and affinity post-move due to the increase in group size.

Table 2. Interaction rates, which represent each individual's interaction with each of the other individuals, were calculated in *SOCPROG* for symmetric social behaviors pre-move (A) and post move (B)

(A)

		Dolphin					
		A	D	I	L	N	V
Dolphin	A	--	9	0	0	5	1
	D		--	0	0	13	0
	I			--	26	0	2
	L				--	0	1
	N					--	0
	V						--

(B)

		Dolphin					
		A	D	I	L	N	V
Dolphin	A	--	8	42	24	0	3
	D		--	10	11	11	1
	I			--	52	0	1
	L				--	5	5
	N					--	0
	V						--

Table 3. Network analysis results calculated in *SOCPROG* for symmetric social behaviors pre-move (A) and post-move (B)

(A)

Dolphin	Strength	Eigenvector centrality	Affinity
A	15	0	19.47
D	22	0	16.77
I	28	0.71	25.36
L	27	0.7	27.11
N	18	0	20.06
V	4	0.08	24.5

(B)

Dolphin	Strength	Eigenvector centrality	Affinity
A	77	0.5	92.16
D	41	0.2	71.2
I	105	0.62	82.84
L	97	0.56	81.33
N	16	0.06	58.5
V	10	0.06	86.2

Asymmetric Social Behavior

All Nonsexual Contact Behavior—These data analyses included all tactile contact behaviors (touches/rubs) excluding sexual contact. The interaction rates that were calculated using *SOCPROG* for pre- and post-move are shown in Table 4. There was a significant difference in the interaction rates for nonsexual contact behaviors pre-move (M = 15.45, SD = 10.59) and post-move (M = 1.82, SD = 0.39): t(21) = 6.19, $p < 0.001$. Pre-move

(Table 4A), the nonsexual contact interaction rates were highest for Ivan initiating toward Largo and Vixen initiating toward Ivan in Pool A, and Astro initiating contact behaviors toward Doris in Pool B. Post-move, the nonsexual contact interaction rates changed in terms of new dyad formation (Table 4B). The highest interaction rate (45) was for Ivan initiating nonsexual contact (tactile behaviors/rubs/touches) toward Astro. The second highest interaction rate (31) was Astro initiating nonsexual contact toward Ivan.

David's (1987) score was calculated for all nonsexual contact behaviors post-move. Table 5 lists the individuals with the more dominant indices to the least dominant indices. Largo and Ivan were the most dominant individuals in initiating nonsexual contact behaviors.

Sexual Contact Behavior—There were only 22 sexual contact events, all of which occurred post-move. There was significant asymmetry between Ivan and Astro for sexual contact behaviors. Ivan initiated sexual contact toward Astro significantly more than toward any other dolphin in the pool: X^2 (1, N = 22) = 18.00, $p < 0.001$. According to the dominance index calculated using David's (1987) score, Largo was the most dominant individual in terms of initiating sexual interactions as reported in Table 5.

Table 4. Nonsexual contact interaction rates among individuals pre-move (A) and post-move (B)

(A)

		Receiving dolphin					
		A	D	I	L	N	V
Initiating dolphin	A	0	5	0	0	0	0
	D	0	0	0	0	2	0
	I	0	0	0	6	0	0
	L	0	0	0	0	0	1
	N	0	1	0	0	0	0
	V	0	0	6	1	0	0

(B)

		Receiving dolphin					
		A	D	I	L	N	V
Initiating dolphin	A	0	4	31	3	0	4
	D	5	0	1	5	5	1
	I	45	1	0	14	1	0
	L	3	6	7	0	1	1
	N	2	6	0	0	0	1
	V	2	2	0	0	2	0

Chase Behavior—Interaction rates were calculated for chase behavior pre- and post-move using *SOCPROG* (Table 6). There was a significant difference in the interaction rates for chase behavior pre-move (M = 17.26, SD = 7.67) and post-move (M = 2.33, SD = 1.30): t(26) = 11.88, $p < 0.001$. Pre-move, the highest interaction rate for chase was Ivan toward Largo (8). Ivan initiated chases toward a new social partner after the move. Post-move, Ivan also had the highest interaction rate for chase behavior, but this time it was directed toward a new social partner: Astro (88).

To test for asymmetry in chase behavior post-move, chi-square tests were calculated. There was not enough chase behavior pre-move to calculate chi-square statistics using *SOCPROG*. However, post-move, Ivan initiated chases toward Astro significantly more so than toward any other dolphin in the pool: X^2 (1, N = 234) = 69.06, $p < 0.001$, demonstrating an asymmetric relationship. Noah also significantly initiated chase behavior toward Doris: X^2 (1, N = 234) = 3.77, $p < 0.001$, while Vixen significantly initiated chases toward Noah: X^2 (1, N = 234) = 5.00, $p = 0.03$. The David's (1987) score dominance indices for chase behavior are reported in Table 5. Ivan was the most dominant individual for initiating chase behaviors post-move.

Aggressive Behavior—Aggressive interaction data were only analyzed for the post-move condition due to the lack of aggressive data recorded prior to the combination of the two social groups. Interaction rates were calculated using *SOCPROG* for each individual's interaction with all other individuals for aggressive behaviors (listed in

Table 5. Dominance rankings based on David's (1987) scores in four different contexts, arranged from most to least dominant for each context

Nonsexual contact		Sexual contact		Chase		Aggressive	
Dolphin	David's score	Dolphin	David's score	Dolphin	David's score	Dolphin	David's score
Largo	4.94	Largo	3.00	Ivan	4.63	Doris	2.91
Ivan	4.89	Vixen	1.00	Vixen	1.96	Ivan	2.90
Doris	-1.05	Ivan	0.00	Noah	0.80	Astro	-0.02
Vixen	-2.76	Astro	-4.00	Astro	-0.28	Largo	-1.22
Astro	-2.04			Doris	-1.69	Vixen	-2.18
Noah	-3.06			Largo	-5.42	Noah	-2.40

Table 6. Interaction rates among individuals pre-move (A) and post-move (B) for chase behavior

(A)

		Receiving dolphin					
		A	D	I	L	N	V
Initiating dolphin	A	0	1	0	0	0	0
	D	2	0	0	0	2	0
	I	0	0	0	8	0	0
	L	0	0	2	0	0	0
	N	2	5	0	0	0	0
	V	0	0	3	2	0	0

(B)

		Receiving dolphin					
		A	D	I	L	N	V
Initiating dolphin	A	0	9	7	7	1	5
	D	8	0	1	15	3	4
	I	88	3	0	13	2	3
	L	4	10	13	0	1	3
	N	1	10	1	2	0	4
	V	2	2	4	5	7	0

Appendix 1). The highest interaction rates were for both Doris and Ivan initiating aggressive behaviors toward Astro (5) and for Doris also initiating toward Vixen (5) (see Table 7).

A chi-square test for asymmetry demonstrated that Doris was aggressive toward Vixen: X^2 (1, N = 46) = 5.00, $p < 0.05$. This indicated that there was asymmetry in the probability of the interactions between Doris and Vixen, with Doris initiating significantly more aggressive behavior toward Vixen than vice versa. However, despite having the greatest aggressive interaction rate, the chi-square test asymmetry results were nonsignificant for Astro and Doris. David's (1987) score dominance indices were calculated for all aggressive behaviors post-move and reported in Table 5. Doris and Ivan had the highest David's (1987) scores: 2.91 and 2.90, respectively. Therefore, they were the most dominant individuals for aggressive interactions.

Table 7. Interaction rates among individuals post-move for aggressive behaviors

		Receiving dolphin					
		A	D	I	L	N	V
Initiating dolphin	A	0	4	2	4	0	2
	D	5	0	0	0	1	5
	I	5	3	0	4	0	0
	L	2	0	1	0	1	1
	N	0	0	2	0	0	3
	V	2	0	0	2	3	0

Discussion

Our results demonstrate that the integration of two social groups increased overall social interactions and allowed the opportunity for new social partners to form, but it did not change stable interaction patterns present in the smaller groups, even given the small sample size. Specifically, Ivan and Largo maintained high levels of positive social interactions after the integration of the two groups; however, both animals also engaged in frequent interactions with new members of the larger group. The change in social interaction rates was further evident in the switch from Largo, Ivan, and Vixen having the highest affinity pre-move, to Astro having the highest affinity score post-move. This change has to do with the formation of the larger social group and Astro's affinity increasing greatly by his increased interaction rates (asymmetric and symmetric) with Ivan. This pattern of social interaction may reflect the fission-fusion nature of dolphin societies (Connor et al., 2000b; Marino, 2002) and suggests that the processes which drive social activity among wild rough-toothed dolphins also influence the social structure of captive rough-toothed dolphins.

The formation of new social dyads was reflected in symmetric and asymmetric social interactions. One particularly interesting new social partnership was formed between Ivan and Astro, two juvenile males. These two spent a greater percentage of time interacting with each other than with any other individuals and also demonstrated a high social interaction rate (42) for symmetric social behaviors. In addition, for nonsexual contact behavior, Ivan and Astro's interaction rates were higher than any other dolphin pair in the pool. This suggests that Astro, one of the newly translocated dolphins, might have been seeking information from an unfamiliar resident dolphin, Ivan (e.g., Dudzinski, 1998; Connor et al., 2006). When change in group composition occurs, social interactions with conspecifics can expedite acclimation to a novel environment (Pinter-Wollman et al., 2009). In such situations, tactile contact among group members might also serve to facilitate social bonds; for example, among bonobos (*Pan paniscus*), a young female emigrating to a new community must first be invited to engage in genital-genital rubbing with an older, longer-term female resident of that group (Strier, 2003); after this contact, the two females become bonded, and the younger female becomes a companion of the older resident female. Tactile associations with familiar conspecifics in a novel environment may provide protection against unfamiliar aggressive conspecifics (Cheney & Seyfarth, 1983; Jack & Fedigan, 2004) and function to reduce any potential stress caused by relocation. Of course, the nature of interactions is often quite complex: Pinter-Wollman et al. (2009) found that translocated African elephants (*Loxodonta africana*) associated less with unfamiliar local residents and more with familiar conspecifics initially but observed that the social segregation decreased over time. Elephants, like many dolphin species, live in fission-fusion societies, and findings indicate that translocated elephants can integrate into an existing social setting over time (Moss & Poole, 1983; Wittemyer et al., 2005; Pinter-Wollman et al., 2009). Forsman et al. (2007) found that migratory birds will often seek out information from unfamiliar residents in a novel environment since the local, though unfamiliar, residents have information about the new habitat that familiar conspecifics may not.

In addition to being the most social of the rough-toothed dolphins, Ivan and Astro exhibited the highest interaction rates for nonsexual contact behaviors. During adolescence, juvenile dolphins transition to spending more time in contact with peers than with their mother (Pryor, 1990). As dolphins develop from calves to juveniles and adults, they engage in contact behaviors with individuals of their same gender and age class (Sakai et al., 2006; Paulos et al., 2008; Dudzinski et al., 2009, 2010). For instance, a longitudinal study of contact behavior in Indo-Pacific dolphins (*Tursiops aduncus*) and Atlantic spotted dolphins (*Stenella frontalis*) indicated that juveniles of both species engaged in tactile contact almost exclusively with other same-sexed juveniles (Dudzinski et al., 2009, 2010). The high occurrence of nonsexual contact behavior between Ivan and Astro suggests this same-sex pattern of tactile contact among rough-toothed dolphins as well.

Male-male alliances have been observed as one of the strongest associations among adult bottlenose dolphin populations in both Sarasota Bay, Florida (Wells et al., 1987), and Shark Bay, Australia (Connor et al., 1992). This strong association is believed to develop when males are juveniles, and it strengthens as they mature (Wells, 1991; Möller et al., 2001). The increase in social interactions between Ivan and Astro is consistent with the notion that dolphins form long-term stable relationships with members of the same sex (Smolker et al., 1992; Connor et al., 2000a). The social bonds formed between males in the wild may help facilitate mating behaviors in sexually mature adults (Connor et al., 2000a). Furthermore, the heightened sexual behavior between Ivan and Astro is consistent with observations of wild juvenile male bottlenose dolphins (Mann, 2006). This socio-sexual behavior observed between juvenile males is likely an opportunity to practice mating (Connor et al., 2006) as well as another modality to enhance alliance formation. It is possible that post-move, the two juvenile males in this study increased their social "alliance" as a natural effect of their age and sex. This new partnership was consistently observed only 1 mo after the social integration and appeared to remain stable over the next 4 mo of this study.

In many nonhuman primate species, higher-ranking males exhibit more aggressive behavior than lower-ranking males (Nunn, 2000). However, dominance relationships among dolphins can be flexible (Johnson & Norris, 1986). For example, individual associations between some male dyads do not remain stable over the years (for bottlenose dolphins: Östman, 1991; Smolker et al., 1992; Samuels & Gifford, 1997; for Atlantic spotted dolphins: Dudzinski, 1996). Social relationships between individuals are dynamic and highly dependent on social context (Connor et al., 2000) as well as sex, age, and body size (e.g., Wells et al., 1980; Östman, 1991; Samuels & Gifford, 1997). Two captive males observed in Samuels & Gifford's (1997) study shared a dynamic dominance relationship that was characterized by periods of stability and low-level aggression. Although there are no documented differences among delphinids with respect to the types of aggression displayed between the sexes, large males are generally considered the most aggressive (Caldwell & Caldwell, 1977), most frequently directing aggressive behavior at peers and immature males (Samuels & Gifford, 1997; Dudzinski et al., 2002; Scott et al., 2005). For this reason, we expected Noah to be the most aggressive dolphin in the group, followed by the two juvenile males, Ivan and Astro. However, it was Ivan who exhibited the most aggressive behavior of the males. This heightened display of aggression by Ivan parallels the findings of a study conducted by Holobinko & Waring (2009) in which the rates of aggression were higher for juveniles (61%) than for other age classes (39%) among captive bottlenose dolphins. Ivan's high dominance standing based on his David's (1987) scores could be linked to his high interaction rates for all asymmetric behaviors. Interestingly, Noah (the adult male) was the only animal to initiate aggressive behaviors toward Ivan.

In their studies of wild populations in Shark Bay, Australia, Scott et al. (2005) found that females receive aggression more often than males, primarily from juvenile and adult males. We observed a similar pattern in our study in which both juvenile males aggressed upon an adult female (who, consequently, had the highest aggressive dominance ranking determined by David's [1987] score). These results also parallel that of Blanchard et al. (1984), who found that male lab rats aggressed more toward female opponents who had aggressed upon them than toward other male opponents. Our results indicate that this might be true for dolphin societies as well.

Given that adult females are likely to form stable associations within a group in the wild (Wells, 1991; Mann et al., 2000), we expected Doris and Vixen to interact with one another socially after the move. This did not occur for any affilliative interactions, perhaps because the ecological pressures that usually drive female grouping in the wild, such as protection from male harassment and alloparental care for calves (Wells, 1991; Mann & Smuts, 1999; Gibson & Mann, 2008), were not present in this group. Neither Doris nor Vixen had any offspring, and there was a minimum threat from male harassment since only one of the males, Noah, was sexually mature. Although the heightened aggression between Doris and Vixen may contradict previous research that indicates female dolphins do not compete aggressively (e.g., McBride & Hebb, 1948; Mann & Smuts, 1999), our results are consistent with more recent observations of captive bottlenose dolphins. In Samuels & Gifford's (1997) study, increased agonism was observed between newly introduced females, and Weaver (2003) found that female pairs displayed higher rates of aggression than male or intersex pairs. Since Doris and Vixen were not housed together prior to the combination of the two social groups, they were newly associated. Despite Ivan being the most aggressive male in the group, Doris had the highest aggressive interaction rate of the group overall. The increased initiation of aggressive behavior conducted by Doris may be due to her age (an older adult dolphin) and her higher status in the dominance hierarchy.

In conclusion, some of the rough-toothed dolphins (Ivan and Largo) exhibited stable social relationships that persisted after the group size was increased. In addition, new social relationships developed after the merge of the two groups. The strongest new social dyad (Ivan and Astro) was reflected in overall social, sexual contact, nonsexual contact, chase, and aggressive interaction rates. Understanding animals' behavioral dynamics in relation to changes in habitat and group size is important for developing conservation tools and enhancing our basic understanding of animals' acclimation to novel environments (Pinter-Wollman et al., 2009). Research in captive settings can lead to a greater understanding of dolphin social behavior, particularly in unique conditions such as those provided by the combination of two social groups of a little studied species. The processes involved in social interactions among wild rough-toothed dolphins might also be mirrored in the social interactions of captive rough-toothed dolphins. According to Dudzinski (2010), systematic behavioral observations of captive dolphin social groups, when compared to data collected on wild populations, could "elucidate details of dolphin associations, behavioral interactions, and social life" (p. 567). For example, Dudzinski et al. (2012) directly compared tactile contact between dolphins from a captive facility and two wild populations, and found some site-specific behaviors and some individual differences in self rubbing vs social rubbing behavior for each animal.

Additional analysis of asymmetric tactile interactions among this social group will provide a greater understanding of the relationship between specific dyads and of the social group as a whole. Specific types of contact behaviors can be used in certain contexts (i.e., Dudzinski, 1996; Paulos et al., 2008; Dudzinski et al., 2009). A more detailed analysis of the specific types of nonsexual contact behaviors observed in this group of rough-toothed dolphins would increase our understanding of the relationship between dyads and the contexts in which certain contact behavior may occur.

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Appendix 1. Social behaviors and definitions

Behavior	Operational definition
Symmetric Social Behaviors	
Pair swim	Two dolphins swim, often in synchrony, within one body length of each other
Social play	Play with conspecifics (Burghardt, 2005) that does not include any additional forms of enrichment (i.e., bubbles, water, objects)
Group social ball	Two or more dolphins swim around each other and appear to be "wrestling" (often associated with play) such that it is extremely difficult to identify the individual behaviors in which each animal is engaged
Asymmetric Social Behaviors	
Nonsexual contact	
Tactile	One dolphin makes contact with or actively rubs another dolphin
Sexual	
Sexual contact	Sex-related behaviors such as genital inspection or genital rubs and/or mating; can be between or within sexes
Chase	
Chase	Dolphin swims quickly and actively in persistent pursuit of another dolphin(s)
Aggressive	
Hit	Initiating dolphin rubs his or her body along the entire body length of the receiving dolphin
Mouth/Bite	One dolphin opens and closes mouth quickly and with force around another dolphin anywhere on body; nipping or biting motion even if no contact is made
Threat	Initiating dolphin touches or rubs his or her lateral side against the lateral side of the receiving dolphin