Agonistic Interactions and Dominance Relationships in Three Groups of Captive Odontocetes: Method of Assessment and Inter-Species/Group Comparison

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Abstract

Social group dynamics are known to impact odontocetes' health and welfare in captivity. Social dominance and agonistic interactions that occur to establish and maintain these relationships might express themselves differently between species and groups, and could be used to monitor social changes. This is the first comparative and quantitative study of agonistic interactions and dominance relationships among three groups of captive odontocetes—Yangtze finless porpoises (YFPs; *Neophocaena asiaeorientalis asiaeorientalis*), East Asian finless porpoises (EAFPs; *Neophocaena asiaeorientalis sunameri*), and bottlenose dolphins (BDs; *Tursiops truncatus*)—and the first use of two methods, including the Elo-Rating Method, to assess dominance in odontocete groups. In this article, we also describe agonistic behaviours in finless porpoises (FPs) for the first time. Agonistic behaviours differed among groups, and BDs' agonistic encounters lasted significantly longer than FPs' ($\chi^2 = 441.77$, $df = 2$, $p < 0.0001$). In the three groups, males were more frequently engaged in agonistic interactions than females (YFPs: $\chi^2 = 8.1144$, $df = 1$, $p = 0.004392$; EAFPs: $\chi^2 = 6.3229$, $df = 1$, $p = 0.01192$; and BDs: $\chi^2 = 4.5977$, $df = 1$, $p = 0.03201$). Unlike BD females, YFP females initiated agonistic interactions more frequently than males. YFPs and BDs engaged more often in agonistic interactions when an unusual social event occurred (e.g., reunion of social groups or introduction of new animals). Finally, there was no influence of sex in the dominance hierarchy of FPs whereas BD males were dominant over females in this study. In FPs, younger individuals were found to be the highest ranked for both sexes. We recommend daily monitoring of agonistic behaviour and social dominance in captive odontocete groups using the method described herein for detecting social changes early that might develop to threaten an animal's physical and psychological health and welfare.

Key Words: agonistic behaviour, bottlenose dolphin, *Tursiops truncatus*, odontocete, finless porpoise, *Neophocaena asiaeorientalis* sp., social dominance

Introduction

In captive groups, solving welfare problems requires understanding the animals' social behaviour, group dynamics, and individual differences. Understanding the social hierarchies in captive animal groups is of both ethical and practical importance for which records on these social changes can aid in predicting and preventing future disruptions and inform strategies to improve long-term management. Social dominance can impact the health and welfare of captive odontocetes through the agonistic interactions that occur to establish and maintain it (McBride & Hebb, 1948; Tavolga, 1966; Tayler & Saayman, 1972; Samuels & Gifford, 1997; Galindo & Broom, 2000; Rees, 2015). Health problems can be difficult to diagnose in captive odontocetes (Rose et al., 2009) due to subtle or masked clinical signs. Changes in dominance status or an increase in the incidence of agonistic behaviours could be the first signs of health or welfare problems in social groups that could lead to physical or psychological harm for individuals if not detected and managed at early stages (Waples & Gales, 2002). The ever-changing and sensitive nature of group dynamics makes it crucial to monitor social groups on a daily basis (Maple & Perdue, 2013). A recent review highlighted the need to investigate how husbandry decisions and management affect the social life of captive marine mammals and to create husbandry guidelines for each species in captivity (Brando et al., 2018). Therefore, for species that lack research, it is crucial to conduct studies to understand them better and to participate in husbandry improvement. To our knowledge, no consistent method has been proposed yet for daily monitoring of agonistic behaviours and social status in captive odontocetes groups.

Agonistic Interactions and Social Dominance

Agonistic encounters in social animals are defined as interactions involving aggressive and/or submissive behaviours (Scott & Fredericson, 1951). Social dominance and agonistic interactions are thought to be closely related (Caldwell & Caldwell, 1972; Francis, 1988), with the observation of dyadic agonistic encounters required to assess dominance relationships (Samuels & Tyack, 2000). The dominance status of an individual describes its particular rank in the dominance relationships of a group. This status is thought to be dependent on a combination of individual attributes (e.g., age, gender, size, etc.) and extrinsic factors (e.g., available resources, prior experience, group composition, etc.) (Clutton-Brock et al., 1982; Rutberg, 1983; Frank, 1986; Francis, 1988; Le Boeuf & Reiter, 1988). Dominance relationships can vary in stability and are often linked with individual cooperation, reproductive success, or access to resources (Dewsbury, 1982; Harcourt, 1987; Samuels et al., 1987; Noë et al., 1991; Bulger, 1993). Dominance and agonistic behaviours are well documented for some species, especially primates (Maslow, 1936; Kawai, 1958; Rowell, 1966; Kaufmann, 1967; Poirier, 1970; Rose et al., 1971; Hausfater et al., 1982; Sapolsky, 2005; Habig & Archie, 2015; Wittig et al., 2015) whose aggression and wounding are associated with social power, displacement, fragmentation, and grooming reciprocity, as well as manipulation of the group (McCowan et al., 2008).

Agonistic Interaction and Dominance in Odontocetes

Odontocetes exhibit complex social organizations that range from fission-fusion to matriarchal, each with both affiliative and agonistic behaviours displayed between and among individuals (Norris, 1967; Connor et al., 2000a). Most of the knowledge on agonistic behaviour in these species originated from studies of captive bottlenose dolphins (*Tursiops truncatus*; Tyack, 2000) for which both aggressive and submissive behaviours have been observed. The behaviours observed during odontocetes' agonistic interactions include visual displays such as S-postures or jaw opening (Dudzinski, 1998; Horback et al., 2010; Hill et al., 2015), pursuit behaviours such as chasing and escaping (Connor et al., 1992a, 1992b; Holobinko & Waring, 2010), and contact behaviours such as biting and body hitting (Samuels & Gifford, 1997; Connor et al., 2000b). The only quantitative assessment of agonistic behaviours in bottlenose dolphins reported 0.026 male-male interactions per minute, 0.022 female-male interactions per minute, and 0.006 female-female interactions per minute (Samuels & Gifford, 1997).

Dominance hierarchies involving aggressive behaviours have been reported in captive odontocete groups (bottlenose dolphin: Samuels & Gifford, 1997; Waples & Gales, 2002; Birgersson et al., 2014; Frick, 2016; Indo-Pacific bottlenose dolphin [*Tursiops aduncus*]: Waples & Gales, 2002; beluga [*Delphinapterus leucas*]: Recchia, 1994; Evans, 2015; killer whale [*Orcinus orca*]: Hargrove & Chua-Eoan, 2015; Anderson et al., 2016; rough-toothed dolphin [*Steno bredanensis*]: Pepper Reid, 2016). Among these studies, only one quantitatively assessed dominance (Samuels & Gifford, 1997); others mentioned it but did not study it in detail. Animals of different species or from different facilities may not display the same behaviours or dominance hierarchies (Wood, 1986). Probably due to logistical constraints, no field or captive study has compared odontocete species or groups' agonistic behaviour and dominance. Describing and considering each species' agonistic behaviours might provide for more accurate species-specific monitoring of each group, which could offer options related to maintenance or improvement of their management and welfare. To do so, accurate methods are needed that can be easily adapted to most facilities for daily assessment of agonistic behaviours and dominance relationships. Comparing species' characteristics of agonistic behaviour and dominance expression might also contribute to our understanding of how the natural environment might have shaped these features. Features of social hierarchies could differ with, for instance, different dynamics and factors that might impact an individual's social rank depending on the species and/or group. Among social dominance assessment methods, some might be accurate for a species/group but not for another, and comparing results from several methods might be helpful to determine the best method(s) to use for each group.

The Elo-Rating Method—a method using a history of wins and losses that has been frequently used to assess dominance hierarchies in primate groups (Cassalette et al., 2016; da Silva et al., 2016; Pusey et al., 2016; Schoof et al., 2016; Wooddell et al., 2016; Newton-Fisher, 2017)—has not been applied as a tool to augment our understanding of any odontocete social hierarchy. This method could be a useful tool, in complement to Samuels & Gifford's method (1997), to examine in detail an individual's potential dominance status within a group on a daily or weekly basis.

Bottlenose dolphins (BDs) and narrow-ridged finless porpoises (*Neophocaena asiaeorientalis*) are commonly kept in captivity in Asia (Zhang et al., 2012). The narrow-ridged finless porpoise includes the East Asian finless porpoise (EAFP; *N. a. sunameri*), which lives in marine

environments, and the Yangtze finless porpoise (YFP; *N. a. asiaeorientalis*), which is found exclusively in the Yangtze River (Jefferson & Wang, 2011). These small odontocetes exhibit different social structures and, thus, require different captive management than the commonly kept and well-studied BDs; however, few studies have investigated finless porpoises' (FPs) behaviour in captivity. Investigating group- or species-specific characteristics related to agonistic behaviour and dominance will contribute to a better understanding of each species' group dynamics, as well as aid in their management. In addition, FPs are classified as endangered (critically endangered for the YFP) species under the criteria of the International Union for Conservation of Nature's (IUCN) (2013) *Red List of Threatened Species*, and, despite a captive breeding program started in 1996 for the YFPs, few calves have been born and survived in both species (Yang et al., 1998; Wang et al., 2005; Deng et al., 2019). Understanding the social behaviour of these animals and their social hierarchies will aid in their group management, improve welfare, and, in turn, increase chances of breeding success. Our first goal was to describe agonistic behaviour in these three odontocetes (YFPs, EAFPs, and BDs) at different facilities. Second, we collected quantitative behavioural data to describe potential dominance relationships within each of these three groups using two different methods.

Methods

Subjects, Housing, and Group Composition

Observations were conducted from early September 2017 to late March 2018. Five YFPs were observed in the Baiji Dolphinarium, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan (Table 1). When all individuals were housed together, YFPs resided in a kidney-shaped pool (20 m long × 7 m wide × 3.5 m deep), linked by a corridor to a round pool (10 m diameter × 3.5 m depth). These two pools were separated by a gate allowing animals to see each other when males and females were separated (females in the kidney-shaped pool and males in the round pool), as well as when one individual, "Duoduo," was apart from others (Duoduo in the round pool and others in the kidney-shaped pool). Two individuals, "Taotao" and "F7," were moved to another disconnected round pool (13.5 m diameter × 3.5 m depth) on 2 February 2018 (Figure 1). These changes in social grouping mainly occurred to manage three pregnant females.

Four EAFPs and five BDs were observed in Haichang Polar Ocean World, Wuhan (Table 1). EAFPs were always kept in a rectangular pool (13.75 m long × 8 m wide × 5.8 m deep), and BDs

were housed in a three-pool complex, with two round pools (5 m diameter × 8.86 m deep) connected to the main pool (27.44 m long × 12 m wide × 6 m deep). Depending on the observation session, animals had access to one, two, or all of the pools. On 16 January 2018, a new female BD arrived at the facility and was placed with the other female on 23 January 2018. When males and females were separated, females were kept in one round pool and males in the other round pool and/or in the main pool.

YFPs were subject to four to six training sessions daily with no public presentation but occasional visitors who were allowed to watch animals both from the surface and from underwater windows. YFPs were fed between 3 and 3.5 kg of thawed (basilewsky [*Sinipercca chuatsi*]) and/or live fish per day during training sessions. EAFPs were not trained but had three feeding sessions daily with a total feed of between 2.5 and 3 kg of thawed fish (i.e., capelin [*Mallotus villosus*], herring [family Clupeidae], squid [superorder Decapodiformes], mackerel [family Scombridae], greasyback shrimp [*Metapenaeus ensis*], and loach [superfamily Cobitoidea]) per day, sometimes including live fish. BDs participated in three training sessions and two public presentations daily during which they were fed between 10 and 13 kg of thawed fish (i.e., capelin, herring, squid, and mackerel).

Data Collection

One month of preliminary *ad libitum* data were collected as a pilot study to identify and become familiar with each individual and, based on the literature, to build a common ethogram for the three species (Table 2). For the formal research protocol, each group was observed two days a week with three 15-min observation sessions per day (early morning, noon, and early afternoon). Observations were conducted between training sessions, public presentations, and feedings.

Observations consisted of video and voice recordings, using two to six cameras to monitor each group depending on pool configuration. For YFPs, four cameras were used to monitor the kidney-shaped pool: two cameras placed in front of underwater windows and two overhead monitoring cameras (one of them also allowed monitoring of the connected round pool). One camera was placed in front of an underwater window to monitor the connected round pool, and two underwater cameras (i.e., in the pool) and one overhead camera were monitoring the disconnected round pool. For the EAFPs, two Xaoyi 4K cameras were placed in front of underwater windows. For BDs, two Xiaoyi 4K cameras were placed in front of a bubble-shaped window situated 5 m deep in the main pool. Three other Xiaoyi 4K cameras were

Table 1. Catalog of individuals in this study (YFP = Yangtze finless porpoise, EAFP = East-Asian finless porpoise, and BD = bottlenose dolphin); M = male, F = female, NA = not available, and IHB = Institute of Hydrobiology.

Name	Species	Sex	Age (year)	Weight (kg)	Length (m)	Facility	Prior rank**
Duoduo	YFP	M	8	NA	1.57	Baiji Dolphinarium, IHB	High
F7*	YFP	F	8	NA	1.45	Baiji Dolphinarium, IHB	High
F9*	YFP	F	8	NA	1.45	Baiji Dolphinarium, IHB	Medium
Taotao	YFP	M	14	NA	1.56	Baiji Dolphinarium, IHB	Low
Yangyang*	YFP	F	11	NA	1.47	Baiji Dolphinarium, IHB	Low
Xiaomeng	EAFP	F	4	33	1.43	Haichang Wuhan Polar Ocean Park	Low
Xiaomi	EAFP	M	7	31	1.60	Haichang Wuhan Polar Ocean Park	High
Xiaoxi	EAFP	M	4	41.5	1.49	Haichang Wuhan Polar Ocean Park	High
Xiaozhuang	EAFP	M	7	48	1.70	Haichang Wuhan Polar Ocean Park	Low
Ailun	BD	M	13	280	2.74	Haichang Wuhan Polar Ocean Park	Low
Beila	BD	F	11	250	2.52	Haichang Wuhan Polar Ocean Park	Low
Jiesen	BD	M	14	290	2.69	Haichang Wuhan Polar Ocean Park	High
Luoke	BD	M	13	260	2.70	Haichang Wuhan Polar Ocean Park	High
R*	BD	F	15	260	2.55	Haichang Wuhan Polar Ocean Park	NA

*Pregnant females **Prior rank category given for the following Elo-rating analysis
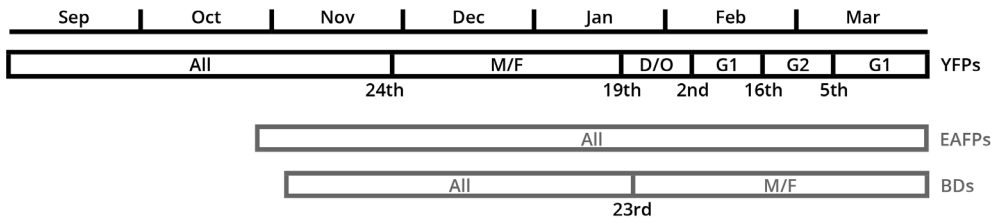

Figure 1. Schedule and grouping during the observation period. All = all the animals together; M/F = males and females separated; D/O = Duoduo separated from other YFPs; G1 = Yangyang and F9 together, F7 and Taotao together, and Duoduo alone; and G2 = Yangyang, F9, and Duoduo together, and F7 and Taotao together.

placed on a bridge between pools to monitor the surface of the main pool and the two round pools. The position of the observation bridge and the small size and depth of the round pools enabled surface-only behaviour recording. Approximately 90% of every pool was covered by cameras that yielded footage with good enough quality to facilitate the analysis. Complementary, direct observation with a voice recorder or with the cameras' audio recording was always used synchronously with the video data collection to ensure identification of each individual and to narrate events for easier analysis. For YFPs, monitoring cameras were perfectly synced using a time display in video files. For EAFPs and BDs, we used the audio recording to synchronize cameras.

Analysis
Videos were visually analysed to document all agonistic interactions, their duration, and the displayed behaviours of involved individuals using event sampling (Altmann, 1974). All statistical analyses were performed using *R*, Version 3.4.1.

Agonistic Interactions and Displayed Behaviours—Agonistic interactions were defined as involving two or more individuals with at least one individual displaying one of the behaviours that were classified as aggressive or submissive (Table 2). An agonistic interaction was considered to have started when one individual displayed one of these behaviours at less than two body-lengths distance from the other individual. When the distance between individuals exceeded two body lengths, the interaction was considered as terminated except during chasing/escaping events. If directly following an agonistic interaction, the involved individuals did

Table 2. Catalog of aggressive and submissive behaviours observed in YFPs, EAFPs, and/or BDs

Behavioral category		Behavior and description	Species	References
Visual behaviors		Actions that are visually displayed; no contact is made between individuals		
	S shape	Individual is arched, its head is up, its back is down, its peduncle is up, and its flukes are down	YFP, EAFP, BD	DeFran & Pryor, 1980; Overstrom, 1983
	Threat	Abrupt back, head, or tail movement directed toward another individual	YFP, EAFP, BD	DeFran & Pryor, 1980; Overstrom, 1983; Samuels & Gifford, 1997; Xiao & Wang, 2005; Holobinko & Waring, 2010
	Nod	Quick up and down repeated head movement directed toward another individual	YFP, EAFP	First described here
	Erratic swim	Individual is swimming through water erratically, usually in circles, and is contained in small area around another individual	BD	Holobinko & Waring, 2010
	Open jaw	Individual opening jaw in direction of another	BD	Holobinko & Waring, 2010; Harvey et al., 2017
	Belly up	Individual's belly fully exposed to the surface of the water in response to another individual's behavior	BD	Holobinko & Waring, 2010
Contact behaviors		Actions/behaviors that result in physical contact or touching between individuals		
	Head to head	Individual takes head-to-head position with another individual or group	BD	Holobinko & Waring, 2010; Harvey et al., 2017
	Sideswipe	Momentary violent body contact resulting from one individual rapidly approaching another and rebounding off of the other's body	BD	Holobinko & Waring, 2010
	Slam	Collision of one animal slamming into another with its body	YFP, BD	Samuels & Gifford, 1997; Xiao & Wang, 2005; Holobinko & Waring, 2010; Harvey et al., 2017
	Bite	Individual bites another individual or opens the mouth close to another individual's body	YFP, EAFP, BD	Samuels & Gifford, 1997; Holobinko & Waring, 2010; Harvey et al., 2017
	Peck	Individual gives one or several quick and short mouth hits on another's body	YFP, EAFP	First described here
	Tail slap	Individual uses its peduncle to ''swat'' another's body or body part (with or without contact)	YFP, EAFP, BD	Samuels & Gifford, 1997; Xiao & Wang, 2005; Holobinko & Waring, 2010; Xian et al., 2010b; Harvey et al., 2017
	Fall on	Individual falls on another animal or its body part at or above the surface	BD	Holobinko & Waring, 2010
	Head butt	Targeted strike with the head	BD	Holobinko & Waring, 2010
	Rostrum hit	Individual hit another with its rostrum	YFP, EAFP, BD	Samuels & Gifford, 1997; Xiao & Wang, 2005; Holobinko & Waring, 2010; Harvey et al., 2017
	Melon hit	Individual hit another with its melon	EAFP, BD	Samuels & Gifford, 1997

Pursuit behaviors		Actions that involve individuals following or moving after other individuals		
	Chase	One or more individuals swiftly following other individuals with a fast swim	YFP, EAFP, BD	Yoshie et al., 1994; Yoshie, 1995; Samuels & Gifford, 1997; Holobinko & Waring, 2010; Harvey et al., 2017
	Charge	One or both individuals approach, head first with fast speed, sometimes making contact	BD	Holobinko & Waring, 2010; Harvey et al., 2017
	U turn	Abrupt U-turn movement; sharp turning motion	BD	Holobinko & Waring, 2010
	Approach-leave-approach	Individual quickly approaches, then leaves and approaches again	BD	Holobinko & Waring, 2010
	Avoid	Abrupt movement of one or more body parts away from another individual; change of body orientation away from it or leaving with no quick speed	YFP, EAFP, BD	Samuels & Gifford, 1997; Holobinko & Waring, 2010; Harvey et al., 2017
	Escape	Abrupt, rapid, and immediate departure to > 1 m from another individual, usually when chased	YFP, EAFP, BD	Samuels & Gifford, 1997; Holobinko & Waring, 2010; Harvey et al., 2017
	Jump	Leap above the water surface to follow another individual or to escape it	BD	Samuels & Gifford, 1997
Sexual behaviors				
	Mount	Individual mounting another, in dorsal, ventral, or side position, abruptly approaching its genital area, whether resulting in genital area contact or not	YFP, EAFP, BD	Holobinko & Waring, 2010; Xian et al., 2010a; Harvey et al., 2017

not separate but started another kind of interaction (e.g., synchronous swimming, swimming together, etc.), and the animals did not display any agonistic or submissive behaviour for the following 10 s, the agonistic interaction was considered to have ended. In this case, the end of the agonistic interaction was defined as the time of the last agonistic or submissive behaviour (we did not include the 10 s with no agonistic behaviour in the interaction duration).

Unlike FPs, BDs engaged in rough social play, which can sometimes appear similar to aggression (Dudzinski, 1996; Johnson & Norris, 1986; Marten et al., 1996; McCowan et al., 2000). We did not record an interaction as agonistic if it contained affiliative behaviour (e.g., rubbing). Conversely, if forceful body contact or high speed chases were observed, the interaction was recorded as agonistic. Context was a useful tool to facilitate categorization of an interaction as play or agonistic; and if any doubt persisted, the interaction was excluded from our analysis.

Frequency and Duration of Agonistic Interactions—Inter-species differences, sex differences, and differences between types of interactions (i.e.,

male-male, male-female, or female-female) for the frequency of agonistic interactions were analysed using Generalized Linear Mixed Models (GLMMs) for Poisson distributed data and Wald Chi squared tests. For YFPs, differences depending on social group were also analysed using GLMMs (social groups did not change for EAFPs and BDs). The inter-species differences on the time spent engaged in these interactions during observation sessions and the duration of interactions were analysed using Linear Mixed Models (LMMs) and Wald Chi squared tests. The identity of individuals and the date were always included in models as random factors. Frequencies and durations were not analysed at the group level (i.e., a sum of frequency and duration of all individuals in the group during an observation session) but at the individual level (i.e., each individual's own frequency and duration during an observation session). Rates of agonistic interactions initiated per hour were calculated for each individual, including both decided and undecided interactions (see below) starting with an aggressive behavior.

Outcome of Agonistic Interactions—Following Samuels & Gifford (1997), an outcome was

determined for every agonistic interaction. If one of the involved individuals only displayed submissive behaviours (e.g., escaping, avoiding, or belly up passive position), the interaction was categorized as "decided," with the submissive animal being the loser and the other being the winner. The winner could either display aggressive behaviours (the winner was described as aggressive) or not (the winner was described as neutral). A neutral winner did not display aggressive or socio-sexual behaviours toward the loser, and the loser displayed at least one submissive behaviour (e.g., loser avoiding winner who exhibited no sign of aggressiveness). If both animals displayed aggressive behaviours, or if the target of aggressive behaviours was not responding to them (i.e., no submissive behaviour), the interaction was categorized as "undecided."

As many socio-sexual interactions occurred in all three species and especially in FPs, we carefully defined which interactions would be included in the analyses. Because mounting is thought to often occur as an aggressive or dominant behaviour in primates and odontocetes (Colmenares, 1991; Ostman, 1991; Pryor & Norris, 1991; Mann et al., 2000; Furuichi et al., 2014; Harvey, 2015), and because during our preliminary observations, we did observe an asymmetry in mounting behaviours in pairs of males, we included one kind of mounting event in the analysis of dominance (they were not counted as agonistic interactions, however). From our preliminary observations, we hypothesized that these mounting events may communicate dominance information between males and, thus, help to maintain dominance without aggression, and maybe even reduce the need for aggression (Frick, 2016). We defined mounting events as dominant when a male (winner) was mounting another male (loser) that did not escape or avoid but stayed floating or lying on the ground or in the water column during the mount (in belly up position or side position). The avoidance or escaping from a male being sexual with another individual (i.e., sexual rubbing, genital looking, and/or mounting) was not recorded as a submissive behaviour since the male was neither aggressive nor neutral; therefore, this type of interaction was not analysed. However, if the individual did not avoid or escape but reacted aggressively, the agonistic interaction and its outcome were recorded and analysed.

Dominance Relationship Assessment—Social dominance between pairs of individuals was assessed using two different complementary methods. First, social dominance relationships were analysed for each pair of individuals following Samuels & Gifford's method (1997), using win-loss percentages (i.e., an individual is dominant if it won at least 75% of decided interactions that occurred with another individual). Social dominance was also assessed in every group using the Elo-Rating Method (Neumann et al., 2011). This modelling method, unlike other methods used to describe linear hierarchies, such as David's scores or Clutton-Brock's index that do not reveal social rank variations during the observed period, yielded an ongoing determination of rank. The Elo-Rating Method, therefore, allowed us to obtain a picture of the variations of the dominance status of individuals over months and, thus, to monitor the dynamics of dominance relationships. This method uses wins and losses to track a rank trajectory and is based on the history of agonistic encounters.

Elo-ratings are attributed to individuals for every fifth interaction, with a higher rating reflecting a higher success in agonistic interactions. Ratings are updated after each encounter using the following formula:

• If higher-rated individual wins,

$$\text{WinnerRating}_{new} = \text{WinnerRating}_{old} + (1\text{-}p) \times k \quad (1)$$

$$\text{LoserRating}_{new} = \text{LoserRating}_{old} - (1\text{-}p) \times k \quad (2)$$

• If lower-rated individual wins (against the expectation),

$$\text{WinnerRating}_{new} = \text{WinnerRating}_{old} + p \times k \quad (3)$$

$$\text{LoserRating}_{new} = \text{LoserRating}_{old} - p \times k \quad (4)$$

where p is the probability of winning for the individual with the highest Elo-rating score at the moment when the interaction occurs. k is a previously chosen number that can be different depending on the type of interaction, its intensity, or the presence of a particular behaviour, for example, or be the same for all interactions. It attributes the number of rating points that an individual gains or loses after an interaction (Neumann et al., 2011). The number of rating points gained or lost will be the same for all interactions if k is the same for all of them; and if k is different depending on a chosen factor (e.g., particular display during the interaction), more points will be gained or lost for certain interactions than for others. The Elo-rating analysis also enables the inclusion of both decided and undecided interactions. However, this method requires an initial "burn-in" period during which the model accumulates observations to attribute rankings to individuals that all start equal. During this period, the model is untrustworthy because all win-loss interactions have the same impact on rank trajectories. Following Newton-Fisher

(2017), to avoid a too long burn-in period, we assigned each individual a prior categorical rank using the results from the preliminary observations and the caretakers' opinions (see Table 1).

For YFPs, each social group was analysed separately. Since social group changes were only separations and reunions (no individual placed in a brand-new group), the last Elo-rating value of each YFP individual in a social group was used as its starting value in the next group. As it was hard to be sure of the role that the intensity of an interaction had in the determination of the social rank, no intensity levels were applied, and a constant default value was applied for k. The BD female "R" was not included in the Elo-rating analysis since she was never involved in agonistic interactions. From the Elo-rating analysis results, we investigated the influence of each individual's gender, age, and size (i.e., length and/or weight, depending on the data available) on their social status in the group.

Results

We conducted 66 observation sessions (990 min) when YFPs were housed together, 51 (765 min) when males and females were separated, 10 (150 min) with Duoduo separated from other individuals, 36 (540 min) in G1 group composition, and 11 (165 min) in G2 group composition (Figure 1). We observed 654 agonistic interactions in total for YFPs, including 399 decided and 255 undecided interactions. Among these interactions, 214 were initiated by an aggressive behavior (Table S1A; supplementary tables are available in the Supplementary Material section on the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index. php?option=com_content&view=article&id=10& Itemid=147), 70 consisted of a submissive behaviour only (winner was neutral; Table S1B), and 115 were "successful" mounts (Table S1C). We conducted 118 observation sessions (1,770 min) for EAFPs with 524 agonistic interactions observed, including 388 decided and 136 undecided interactions. Among these interactions, 179 were initiated by an aggressive behavior (Table S1A), 161 consisted of a submissive behaviour only (Table S1B), and 48 were "successful" mounts (Table S1C). Fifty-eight observation sessions (870 min) were conducted with all the BDs together, and 77 observation sessions (1,155 min) with only the males. Of the 165 agonistic interactions observed, 103 were decided and 62 undecided. Among these interactions, 51 were initiated by an aggressive behavior (Table S1A), 12 consisted of a submissive behaviour only (Table S1B), and 40 were "successful" mounts (Table S1C). For BDs, we observed 264 social play interactions (Table S2).

Agonistic Interactions Characteristics

Agonistic Behaviour Description—All three species were observed displaying aggressive and submissive behaviours. In both species of FPs, direct aggressive behaviours with contact were rare. The most frequent aggressive behaviours in YFPs were tail slaps (*n* = 195; rate = 0.32/interaction; Table S3B) and threats (*n* = 152; rate = 0.21/interaction; Table S3A) for which contact with the target was rare since they often avoided it with a head or body movement. Four strong tail slaps with contact were observed, with three of these by females on males and one by a female on another female with no particular context. The individual giving the tail slap was usually suspended in a vertical position or swimming horizontally and gave a tail slap in the water column. Six biting events were observed in this species—only between the two males—and four of them occurred during socio-sexual interactions. YFPs displayed head, back, and tail threats and occasionally bit other individuals (*n* = 7; rate = 0.006/interaction; Table S3C). Chasing was observed six times in this species (rate = 0.016/interaction; Table S3D). Jaw opening was observed once in YFPs during an agonistic interaction. We observed a male opening his jaw in front of a female once, but we were not able to ensure this was an aggressive display. In EAFPs, the most frequent aggressive behaviours were threats (*n* = 206; rate = 0.23/interaction; Table S3A), chasing (*n* = 80; rate = 0.13/interaction; Table S3D), and tail slapping (*n* = 70; rate = 0.05/interaction; Table S3B). We also observed 50 biting events (rate = 0.018/interaction; Table S3C), four rostrum hits, and two melon hits; all of these behaviours were displayed by males on other males. Another behaviour, one we called the "peck," which was not previously described in FPs, was often observed in agonistic interactions (*n* = 32; rate = 0.03/interaction) with an individual giving one or several rapid and short mouth hits on another's body (usually on the head) without opening its mouth. This behaviour was sometimes preceded by a quick up and down head movement we called the "nod"; the behaviour was displayed while in vertical position, facing the target (these two behaviours also occurred during rough socio-sexual interactions). Individual FPs of both species never displayed aerial behaviours during agonistic interactions (the full interactions were taking place in the water column).

Unlike FPs, BDs' agonistic interactions included forceful contacts and aerial behaviours. The most frequent agonistic behaviours were chasing (*n* = 209; rate = 0.59/interaction; Table S3D) and biting (*n* = 246; rate = 0.62/interaction; Table S3C), but we also observed charging, approach-leave-approach sequences, erratic swimming, and sideswipes. These counts include

behaviors observed during both agonistic interactions and social play. BDs threatened each other ($n = 82$; rate = 0.28/interaction; Table S3A) and occasionally opened their jaws in the direction of another individual during approach-leave-approach sequences or head-to-head displays. BDs did not display tail slaps often ($n = 31$; rate = 0.056/interaction; Table S4B). An S-shape posture was frequently displayed during agonistic interactions in BDs, whereas YFPs and EAFPs rarely showed this posture during this kind of interaction but often did during socio-sexual interactions.

Submissive behaviours were similar between YFPs and EAFPs with "avoiding" being the most frequent in both species ($n_{YFP} = 256$, rate = 0.38/interaction; $n_{EAFP} = 797$, rate = 0.57/interaction; Table S3E). Avoiding often consisted of a change in swimming direction, a departure away from another individual, or a head movement away from it. "Escaping," which consisted of a quick and abrupt departure away from an individual, was less frequent than avoiding ($n_{YFP} = 21$, rate = 0.026/interaction; and $n_{EAFP} = 154$, rate = 0.088/interaction; Table S3F). BDs also displayed these behaviours ($n_{avoid} = 438$, rate = 1.22/interaction; Table S3E; and $n_{escape} = 102$, rate = 0.26/interaction; Table S3F) in addition to jumps, leaps, and U-turns to avoid other individuals, which were never observed in FPs.

FPs' agonistic encounters mostly consisted of a single aggressive behaviour directed toward the target that either responded with a submissive behaviour or gave no reaction. Few interactions in which the target reacted aggressively, resulting in escalating aggression, were observed in both FP species. In BDs, the aggressive individual was often observed displaying several consecutive aggressive behaviours toward the target that would either behave submissively, aggressively, or not react.

Frequency and Duration of Agonistic Interactions—The frequency of agonistic interactions was not significantly different among the species (mean ± SD; YFPs = 2.56 ± 0.204/ind/h, EAFPs = 5 ± 0.312/ind/h, and BDs = 2.12 ± 0.224/ind/h; Wald Chi square, $\chi^2 = 3.7695$, $df = 2$, $p = 0.1519$).

The duration spent engaged in agonistic interactions was significantly different between species ($\chi^2 = 8.8647$, $df = 2$, $p = 0.001189$): YFPs (= 6.88 s ± 0.92 s/ind/h; $\chi^2 = 6.5758$, $df = 1$, $p = 0.01034$) and EAFPs (= 17.6 s ± 1.56 s/ind/h; $\chi^2 = 0.4952$, $df = 1$, $p = 0.02564$) spent significantly less time engaged in agonistic interactions than BDs (= 41.64 s ± 5.68 s/ind/h); and EAFPs spent significantly more time engaged in agonistic interactions than YFPs ($\chi^2 = 42.084$, $df = 1$, $p < 0.0001$).

The duration of agonistic encounters was significantly different among the different species ($\chi^2 = 441.77$, $df = 2$, $p < 0.0001$): YFPs (= 6.88 s ± 0.92 s/ind/h; $\chi^2 = 18.401$, $df = 1$, $p < 0.0001$) and EAFPs' agonistic interactions (= 17.6 s ± 1.56 s/ind/h; $\chi^2 = 21.134$, $df = 1$, $p < 0.0001$) were significantly shorter than BDs' (= 41.64 s ± 5.68 s/ind/h). EAFPs' agonistic interactions lasted significantly longer than YFPs' ($\chi^2 = 39.186$, $df = 1$, $p < 0.0001$). Male YFPs (= 1.98 ± 0.21) were engaged significantly more often in agonistic interactions than females (= 1.55 ± 0.15/ind/h; $\chi^2 = 8.1144$, $df = 1$, $p = 0.004392$); male EAFPs (= 5.87 ± 0.36/ind/h) engaged significantly more often in agonistic interactions than the female (= 3.72 ± 0.42/ind/h; $\chi^2 = 6.3229$, $df = 1$, $p = 0.01192$); and male BDs (= 1.93 ± 0.22/ind/h) engaged significantly more often in agonistic interactions than females (= 0.54 ± 0.17/ind/h; $\chi^2 = 4.5977$, $df = 1$, $p = 0.03201$).

The rates of agonistic interactions initiation of each of the three female YFPs were higher than those of each of the two males (including both decided and undecided interactions; Table S4). In EAFPs, the oldest male, "Xiaozhuang," was the individual with the lowest rate of agonistic interactions initiation. In BDs, the two females and the male, "Ailun," had the lowest rates of agonistic interactions initiation.

The frequency of interactions was significantly different depending on the sex of the two participants for YFPs ($\chi^2 = 24.859$, $df = 2$, $p < 0.0001$), with male-male (= 2.34 ± 0.35/ind/h; $\chi^2 = 22.216$, $df = 1$, $p < 0.0001$) and male-female (= 1.85 ± 0.18/ind/h; $\chi^2 = 17.131$, $df = 1$, $p < 0.0001$) interactions being more frequent than female-female (= 1.25 ± 0.18/ind/h) interactions. Male-male interactions tended to be more frequent than male-female interactions ($\chi^2 = 3.7976$, $df = 1$, $p = 0.05133$). In EAFPs, only one female was present; male-male agonistic interactions (= 5.87 ± 0.48/ind/h) were significantly more frequent than male-female interactions (= 3.80 ± 0.30/ind/h; $\chi^2 = 102.83$, $df = 1$, $p < 0.0001$). In BDs, no agonistic interactions were recorded between females. Male-male interactions (= 3.20 ± 0.38/ind/h) were significantly more frequent than male-female interactions (= 0.69 ± 0.14/ind/h; $\chi^2 = 96.782$, $df = 1$, $p < 0.0001$).

The frequency of agonistic interactions was significantly different depending on the social group for YFPs ($\chi^2 = 19.877$, $df = 4$, $p = 0.0005281$). Agonistic interactions were significantly more frequent when individuals were in the G2 group (= 3.16 ± 0.84/ind/h) than when in the G1 group (= 1.08 ± 0.25/ind/h; $\chi^2 = 16.222$, $df = 1$, $p < 0.0001$) or than when males and females were separated (= 1.21 ± 0.18/ind/h; $\chi^2 = 26.556$, $df = 1$, $p < 0.0001$). No significant differences in the frequency of agonistic interactions were found between other social groups ($p > 0.05$).

There was individual variation in the frequency (Appendix 1) and duration (Appendix 2)

of agonistic encounters (both appendices can be found in the Supplemental Material section of the *Aquatic Mammals* website: https://www.aquatic-mammalsjournal.org/index.php?option=com_cont ent&view=article&id=10&Itemid=147). In YFPs, frequency and duration of agonistic interac-tions increased in the group on days when sepa-rated groups were reunified (19 January and 16 February 2018) and during the four days fol-lowing the reunion. In EAFPs, an increase in agonistic interaction frequency and duration was noticed for all individuals on 16 January 2018. In BDs, frequency and duration of agonistic inter-actions increased for all individuals on the day a new individual was introduced to the facility (16 January 2018) and on the two days following.

Social Dominance
When analysing outcomes of agonistic interactions using percentages of wins and losses for each pair of individuals, the youngest female, F7, was domi-nant over all other YFPs (i.e., she won more than 75% of decided interactions with each individual; Table S5). The female, "F9," was dominant over the female, "Yangyang," and the male, Taotao, but was not higher than the male, Duoduo. The young-est male, Duoduo, and the oldest female, Yangyang, were higher than the oldest male, Taotao. For EAFPs, the youngest male, "Xiaoxi," was higher

than all other individuals; the male, "Xiaomi," was higher than the only female, "Xiaomeng," and the oldest male, "Xiaozhuang." Finally, no domi-nance hierarchy was found between Xiaomeng and Xiaozhuang. For BDs, the males, "Jiesen" and Ailun, were higher than the female, "Beila." The male, "Luoke," was higher than Ailun. When using this method, there was no clear link between Luoke and Jiesen (i.e., no individual won more than 75% of the interactions).

We analysed 563 interactions for YFPs, 573 for EAFPs, and 154 for BDs using the Elo-Rating Method. In YFPs, when all individuals were housed together, the youngest female, F7, had the highest dominance rank, followed by the youngest and largest male, Duoduo (Figure 2). The largest female, F9, was the third-ranked individual, fol-lowed by the oldest female, Yangyang. The oldest male, Taotao, was the lowest in the dominance hierarchy. This hierarchy did not change within sexes when males and females were separated: F7 remained higher than F9 who was higher than Yangyang; Duoduo remained higher than Taotao. When Duoduo was separated from the group, the hierarchy stayed the same with Taotao lower than the three females. After transfer to an unattached pool, F7 was still higher than Taotao, and Yangyang took the first rank above F9 and Duoduo.
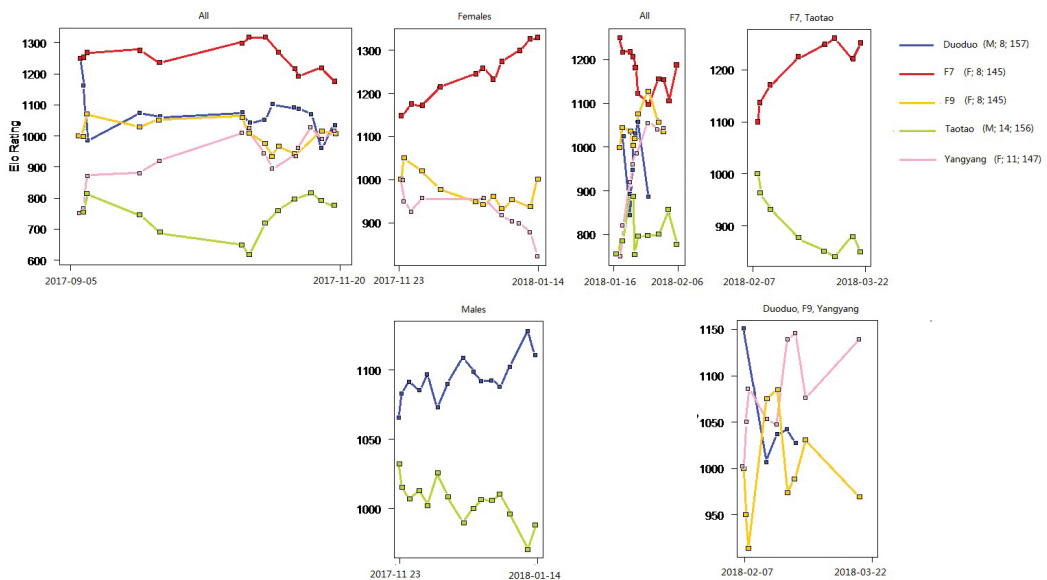

Figure 2. Rank trajectories for YFPs between September 2017 and March 2018 as determined by an Elo-Rating Method that assigns starting Elo-ratings according to prior records of ordered rank categories (high, medium, and low), applied using a negative exponential. Grouping is indicated above each graph. Individuals' features are indicated as "name (gender; age; length)."
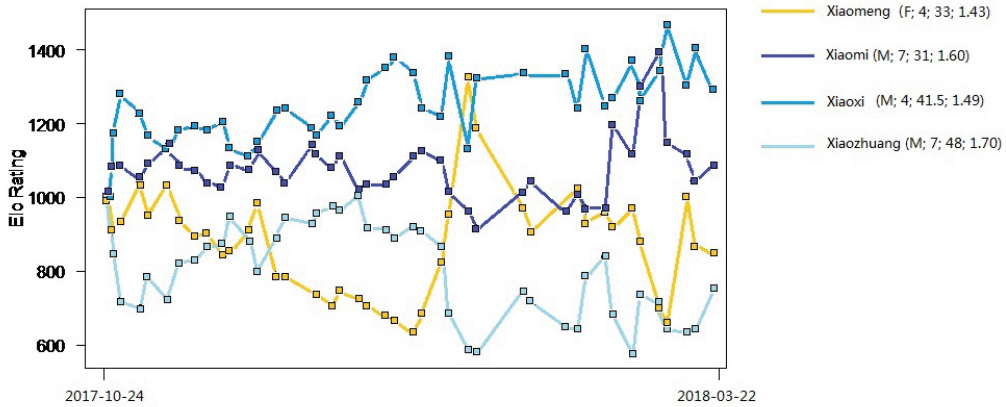
Figure 3. Rank trajectories for EAFPs between October 2017 and March 2018 as determined by an Elo-Rating Method that assigns starting Elo-ratings according to prior records of ordered rank categories (high, medium, and low), applied using a negative exponential. Grouping is indicated above each graph. Individuals' features are indicated as "name (gender; age; weight; length)."
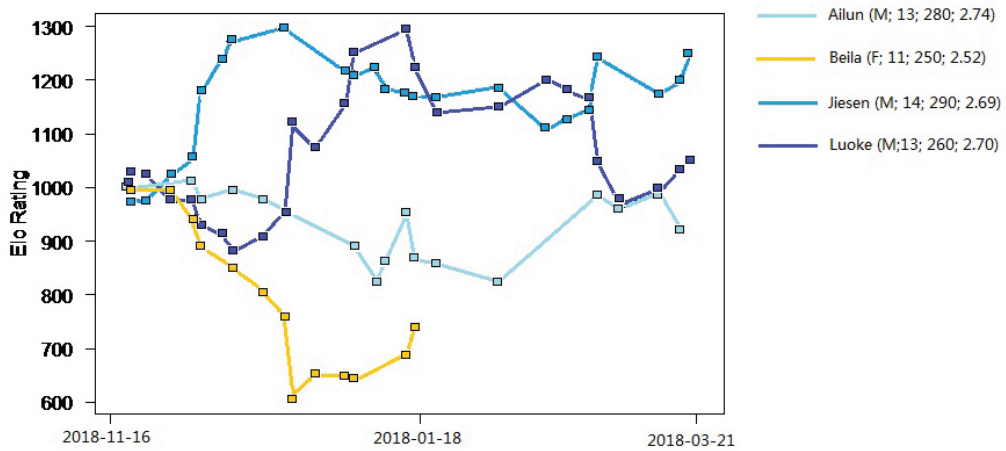

Figure 4. Rank trajectories for BDs between October 2017 and March 2018 as determined by an Elo-Rating Method that assigns starting Elo-ratings according to prior records of ordered rank categories (high, medium, and low), applied using a negative exponential. Grouping is indicated above each graph. Individuals' features are indicated as "name (gender; age; weight; length)."

In EAFPs, the youngest male, Xiaoxi, was the highest ranked, followed by the smallest male, Xiaomi (Figure 3). The dominance relationship between the only female, Xiaomeng, and the largest male, Xiaozhuang, changed during the observation period, with each individual being higher than the other at certain moments and lower at others (the female was higher more often).

In BDs, the three males were higher in the dominance hierarchy than the female, Beila, with Jiesen, the largest male, being the highest, alternating this position with Luoke, the smallest one, and followed by Ailun (Figure 4). As no agonistic interaction was observed between the two females, the female, "R," was not included in the analysis.

Discussion

In this study, we described agonistic behaviours of FPs for the first time. Through the quantitative analysis of agonistic encounters and social dominance in three groups of captive odontocetes, we found inter-species differences in terms of displayed behaviour and duration of interactions for all three. We also highlighted the impact of social events (i.e., management decisions) on frequency and duration of agonistic interactions. This first use of the Elo-Rating Method to assess dominance relations between individuals in three different species and groups provided detailed profiles of variations in individuals' social status during the observation period. Finally, individual features (i.e., sex and age) that seemed to impact individual social status were species-specific. These findings suggest that species and/or groups differ in their expression of agonistic behaviour and social dominance in captivity and, therefore, their study or assessment should be adapted to each species. We also present the first systematic method for daily monitoring of agonistic interactions and social dominance in captive odontocete groups, which could be used as a tool by animal caregivers/managers and researchers alike to detect early social problems that might later on affect the animals' welfare and health.

Agonistic Interactions Characteristics

The BDs' behaviour that we observed and described herein is congruent with previous studies on this species, including threats and body contacts (McBride & Hebb, 1948; Norris, 1967; Ostman, 1991; Connor et al., 1996, 2000a, 2000b; Herzing, 1996; Samuels & Gifford, 1997; Parsons et al., 2003; Weaver, 2003; Blomqvist & Amundin, 2004; Holobinko & Waring, 2010). Regarding FPs, the only existing information on their agonistic behaviours comes from studies of captive EAFPs in which it was suggested that chasing behaviour was frequent during agonistic interactions (Yoshie et al., 1994; Yoshie, 1995); this interpretation was reinforced by our results. This behaviour was also frequently displayed by the EAFPs we studied.

We noticed that the aggressive and submissive behaviours depended on the species. Unlike FPs, whose encounters mainly consisted of threats with only a few body contacts, BDs frequently exhibited forceful body contacts during agonistic interactions. This is congruent with the fact that aggressive behaviour in this species often results in tooth rake marks on the skin (McCann, 1974; Scott et al., 2005; Marley et al., 2013). Conversely, tooth rake marks are apparently rare in FPs (pers. obs. and study site's caretakers' observations).

The frequency of agonistic interactions did not differ among the three species, suggesting that the rate of conflicts in these specific captive conditions is similar. In the literature, rates of agonism vary. Eight aggression events were observed in a total of 1,872 screened hours of killer whales (*Orcinus orca*; 0.004/h) and lasted 12.1 min on average (Graham & Noonan, 2010). The rate of involvement in aggressive interactions was reported to be 0.018/h in female BDs kept with their calves (Scott et al., 2005). Another study reported 88 aggressions by non-provisioned males on females in a total of 208 herding events and 13 aggressions during 58 herding events by provisioned males in this species (Connor et al., 1996). Samuels & Gifford (1997) reported 0.026 male-male interactions per minute (1.56/h), 0.022 female-male interactions per minute (1.32/h), and 0.006 female-female interactions per minute (0.36/h). These rates are lower than those obtained in our study (2.12/h for BDs). In a study of rough-toothed dolphins, the rate of agonistic interaction ranged from 0.8/h to 1.92/h depending on the individuals (Yeater et al., 2013). The higher rate obtained for our BDs might be explained by group composition (only one female with three males here). The facilities' differences in terms of group management and living conditions (e.g., size and shape of pools, enrichment, etc.) could also be a potential factor influencing the animals' behaviour.

Agonistic encounters lasted significantly longer in BDs than in FPs, and BDs also spent significantly more time engaged in these interactions. This difference can be explained by the frequent escalation of conflict in BDs in which the aggressor often displayed several consecutive aggressive behaviours toward the target, resulting in longer interactions. For FPs, agonistic encounters mostly consisted of a single event. EAFPs were engaged in longer interactions than YFPs, which might be explained by the fact that they chased each other more often. The group of EAFPs also included three males while only two were present for YFPs. These interspecific differences in aggressive behaviours could reflect the environment in which the species live in the wild. YFPs inhabit riverine habitats in which they do not have predators but which are restricted areas with limited resources (e.g., food and mating partners), while EAFPs inhabit marine habitats that are not limited in terms of space and resources but in which more predators are found. EAFPs might be more susceptible to predation than BDs due to their small size. In contrast, wild BDs, because of their larger size, might be less vulnerable to predation than EAFPs and might be able to find resources more easily than YFPs. These factors might have led each of these species to adapt their interactions to optimize their survival given these challenges in their environment. BDs might not need to spend as much time as FPs displaying vigilance behaviours, foraging, and

searching for mates, for instance, which would allow them to spend more time interacting.

Another reason that could explain these shorter agonistic interactions in FPs vs those by BDs could be their sociality. BDs' social life has often been studied, both in the wild (Wells et al., 1987; Connor et al., 2000a, 2000b) and in captivity (Tamaki et al., 2006; Yamamoto et al., 2015; Harvey et al., 2017; Serres & Delfour, 2017), and their high level of sociality has often been discussed. Much less is known about FPs' sociality (Sakai et al., 2011). They could be less social than BDs, thus spending less time interacting with their conspecifics, including fewer agonistic interactions. From our observations, and from the few behavioural studies on captive animals (Xiao et al., 2005; Wu et al., 2010; Xian et al., 2010a, 2010b), we suggest that male FPs are highly social, spending a lot of time swimming in pairs and engaging in many socio-sexual interactions. Female FPs engage less frequently in social interactions than male FPs and both sexes of BDs (e.g., socio-sexual and affiliative; Serres, unpub. data, November 2017-October 2018). In addition, FPs were almost never observed playing together the way BDs do (Kuczaj & Highfill, 2005; Kuczaj & Eskelinen, 2014; Serres & Delfour, 2017). Thus, FPs and BDs could have a different level of sociality or their behavioural communication could be different.

In the three species, males engaged more frequently than females in agonistic interactions, and male-male interactions were the most frequent. This result is congruent with results obtained in other studies (Samuels & Gifford, 1997; Scott et al., 2005). However, in YFPs, the rate of agonistic interactions was the highest when each male was housed with one or two females. This pattern might be due to the fact that the two males exhibited a strong relationship and spent a lot of time interacting (mainly socio-sexual interactions and synchronous swimming) when housed together, which could allow them to avoid conflicts with females. When the two males were separated (housed with one or more females), they were more easily targeted by females that were often aggressive toward them.

The frequency and duration of agonistic interactions for each YFP and BD individual peaked on days during which social changes occurred. The reunion of previously separated social groups of YFPs or the introduction of a new BD individual in the facility coincided with increasing agonistic encounters. These social perturbations seemed to impact individuals' aggressive behaviour, which could, in the case of the group reunion in YFPs, be explained by their need to re-establish a dominance hierarchy. For the new BD introduction, the new female was first separated from others by a gate; at this point, an increase in the frequency and duration of agonistic interactions was noticed between the original four individuals. Intraspecific aggression in this species can occur in different contexts and can be influenced by cooperation, reproduction, sexual coercion, and anthropogenic factors (Herzing, 1996; Connor et al., 2000b; Scott et al., 2005). The arrival of a new conspecific, even if separated by a gate, could have been a stressful event for the already-present BDs, potentially resulting in more conflicts (McBride & Hebb, 1948; Caldwell et al., 1968; Caldwell & Caldwell, 1977; Samuels & Gifford, 1997). We noted no specific event on the day the frequency and duration of agonistic interactions were higher in EAFPs, which might suggest a potential social or environmental event that we did not notice.

Social Dominance
Social Dominance and Individual Features—The results obtained using win-loss percentage analyses for pairs and results using the Elo-Rating Method highlighted the same trends in social dominance for FP groups. For BDs, a comparison of the results obtained by the two methods seemed to indicate that both analyses of social dominance, taken separately, might not be appropriate. This result might be caused by a very dynamic social hierarchy, changes in social status being too frequent, or by an absence of clear dominance hierarchy between some or all BDs in this group. Combining the results from both analysis methods was useful because of their advantages and disadvantages: use of percentages allowed investigation of a potential non-linear dominance hierarchy, while the Elo-Rating Method enabled an examination of variations in individual social ranks.

For both FP species, and using both dominance assessment methods, males were not consistently higher than females in the social dominance hierarchy. Depending on the odontocete species, females have been noted to occupy higher or lower dominance positions (BD: Tavolga, 1966; Samuels & Gifford, 1997; killer whale: Anderson et al., 2016; Guarino et al., 2016; rough-toothed dolphin: Yeater et al., 2013), with female BDs usually maintaining stable, age-related dominance relationships (Waples & Gales, 2002; Frick, 2016). In FPs, sex does not seem to impact social status, which might be because female FPs often initiated agonistic interactions. This particularity of FP females might be one reason for the difficulties in breeding these animals in captivity. It could be hard for males to approach females—especially the highest ranked ones.

As described by the only quantitative study of BD social dominance (Samuels & Gifford, 1997), all males (except Luoke when using the Win-Loss Percentage Analysis Method) were higher than females in the hierarchy. No agonistic interaction was observed between the two females, which is in line with observations that male-male and male-female agonistic interactions are more frequent (Samuels & Gifford, 1997; Harvey et al., 2017). In this study, dominance relationships between male BDs did not seem stable, with two males alternating at the highest rank (Elo-Rating Method), and with unclear dominance relationships between pairs (Win-Loss Percentage Analysis Method). This is congruent with the fact that dominance interactions between adult BD males are characterized by periods of stability interspersed with episodes of competition, whereas females' dominance relationships are more stable and constant (Samuels & Gifford, 1997). More generally, relationships between females and those between males exhibit major differences (Smolker et al., 1992; Connor & Krützen, 2015). The difference between the two methods used and the unclear dominance relationships between male BDs might also reveal the elaborateness of BDs' social organization that might be more dynamic and complex than a simple linear dominance hierarchy.

The youngest FPs occupied the highest social rank among both YFPs and EAFPs, which is different to our BD results. The FPs' age seems to have an impact on their dominance status, with younger individuals being higher than older ones. Yeater et al. (2013) studied rough-toothed dolphins, finding that juvenile animals were highest ranked, but the outcome of agonistic interactions was considered by these authors; thus, this hierarchy could reflect aggressiveness more than actual dominance relationships. Even if in the wild older individuals often occupy the highest level of a hierarchy (Rutberg, 1983; Heitor & Vicente, 2009; Cafazzo et al., 2010, 2016), in captivity, young animals may sometimes be observed at higher ranks than older individuals (Rowell, 1974). Young but sexually mature individuals might be more vigorous than older animals and, thus, might win conflicts more often in captivity where the environment is restricted and the experience or skills of older animals is less useful. In our study, all BDs were approximately the same age; therefore, we cannot link age and social status in this species.

In YFPs, as no data on the weight of individuals were available, we could not clearly investigate the influence of size on social status. In EAFPs, the largest male occupied the lowest social position. Conversely, in BDs, the largest male was most often in the highest social position, but he was challenged by the smallest individual. For EAFPs and BDs, we found no link between body size and social status as in other studies (Tavolga, 1966; Acevedo-Gutiérrez et al., 2005); however, our small sample size limits this conclusion, and our findings may only be true for the groups studied here. We also did not investigate the influence of individuals' personality on social dominance, which could have played a role in defining social status (Delfour & Marten, 2005; Highfill & Kuczaj, 2007; Favati et al., 2014; Frick, 2016). Moreover, even if all individuals were adults, the sex ratio was different among species with only one female to three males in EAFPs and BDs but three females to two males in YFPs. This difference in sex ratio could have impacted agonistic behaviours and the observed dominance hierarchies. This dominance assessment was achieved because of the frequent mention of social dominance in dolphin groups, but this hierarchy could be less important than we thought, and the social organization of odontocete captive groups might be more complex and dynamic (Connor et al., 2001), and involve subtle signals that we cannot see or interpret yet.

During our observations, the three YFP females were pregnant, which might have affected the expression of their aggressive behaviour and the hierarchy in the group. However, at the beginning of our observations, the pregnancies would have been in a very early stage, and the Elo-rating results from the first period, when the group was not separated yet, correspond to the dominance pattern observed by trainers and other observers before the females became pregnant. In the last observations of our study period, the primarily lowest female's Elo-rating score increased, exceeding the other female with which she was housed. This could be due to the changes in hormone levels during pregnancy (i.e., testosterone, cortisol, and estrogen; Deng & Serres, unpub. data, 2018).

Social Dominance Differences Between Species/ Groups—Odontocetes' social structure varies from fluid to stable societies (Mann et al., 2000). BDs can be found in groups of up to 100 individuals (Parsons et al., 2003) and live in groups with high levels of fission-fusion dynamics, characterized by rapidly changing associations but with some long-term associations between pairs (Smolker et al., 1992; Connor et al., 1998, 2000b). Little is known about the sociality of FPs in the wild, but it is assumed that the social structure of this species is "undeveloped" and that the mother–calf pair might be the only long-term association (Kasuya & Kureha, 1979; Kasuya, 1999). These differences in social organization and the natural habitat of each species could be contributing

factors to observed differences in social behaviours, especially in agonistic interactions and social dominance (Barrett & Würsig, 2014).

In addition, it could be that captive and wild animals may not behave similarly, and rates of social behaviours (and, therefore, agonistic interactions) could be higher in captive groups, possibly due to the restricted space (e.g., primates: Nieuwenhuijsen & de Waal, 1982; Altmann & Muruthi, 1988). However, elements of dolphin behaviour, including social behaviours, have been reported to be similar in wild and captive delphinids (e.g., Hawaiian spinner dolphins [*Stenella longirostris*]: Wells, 1984; Johnson & Norris, 1994; spotted dolphins [*Stenella attenuata*]: Pryor & Kang Shallenberger, 1991; bottlenose dolphins [*Tursiops* sp.]: Saayman & Tayler, 1977; Samuels, pers. obs. cited in Samuels & Gifford, 1997; Dudzinski, 2010; Dudzinski et al., 2010, 2013).

Information about dominance relationships in the wild is hard to obtain, and no study has shown the presence of such hierarchies in wild odontocetes (Samuels & Gifford, 1997). However, the spatial separation between sexes in some BD populations (Wells et al., 1987) suggests that dominance relationships, if they exist, may not be exhibited in the same way in the wild. In populations where sexes are segregated during most of the year, hierarchies might be present for females and males separately, and these separate hierarchies might change when animals of both sexes are rejoined, making them that much harder to confirm in wild groups. In addition, the fact that relationships between individuals and groups in the wild are thought to be highly dynamic (Lusseau, 2003, 2007); hierarchies, if they exist, might be dynamic as well. The study of the aggressive behaviours and dominance in wild botos (*Inia geoffrensis*), solitary river dolphins, during interactions with humans (Pinto de Sá Alves et al., 2013) highlighted the fact that the presence of a dominance hierarchy in a certain context does not imply its presence in natural conditions. Therefore, the dominance hierarchies in captivity described herein might not be present in the wild. Differences in the management of social groups are present among captive facilities themselves and, therefore, the animals' behaviour and dominance patterns may differ significantly between locations (Wood, 1986; Waples & Gales, 2002). The differences we observed here cannot be clearly attributed to the species but could be specific to the group and the living conditions of these groups. For instance, because of the differences between facilities, applying our methods on another BD group might result in significantly different results.

Assessing Agonistic Behaviour and Dominance to Manage Captive Odontocete Groups

BDs are highly social animals, and social interactions are crucial to maintaining their health (Sweeney, 1990). The sociality of FPs in the wild is not well known yet, but these animals interact frequently in captivity, with socio-sexual behaviours being predominant in males (Yoshie et al., 1994; Nakahara & Takemura, 1997; Xian et al., 2010a; Serres et al., unpub. data, 2018). Social mammals can be subject to psychological stressors (negative or positive) arising from social factors (Weiss, 1972; Rose et al., 1975; Henry & Stephens, 1977; Mendoza et al., 1979; Sapolsky, 1992, 1994; Levine et al., 1997; von Holst, 1998; Haller et al., 1999; Waples & Gales, 2002). Inappropriate captive social groupings, social changes, or instability may increase negative social stressors and result in abnormally high agonistic behaviour in these species (Caldwell & Caldwell, 1977; Wood, 1977; Sweeney, 1990; Waples & Gales, 2002; Lott & Williamson, 2017).

In captive odontocetes, negative stress, revealed by physiological, endocrinological, immunological, and neurological factors (e.g., cortisol and aldosterone) can induce disease and lead to death (Dierauf, 1990; Sweeney, 1990). Stress, as indicated by cortisol levels, was shown to be higher in dolphins kept in closed facilities (i.e., closed pool) than in dolphins kept in open facilities (i.e., pools with access to the sea; Ugaz et al., 2013), and dolphin behaviour has been shown to differ depending on facility (Ugaz et al., 2009). Since captive animals may not be able to always choose the individuals they live with and depending on the shape of enclosures and on the management, which differ between facilities, they sometimes cannot self-separate. Because of this, the captive environment may induce more intense social encounters (including affiliative interactions; Hedinger, 1964).

In captive primates and dolphins, the competition for items that animals seek (e.g., toys, mates, and caretakers' attention), perturbations in dominance relationships, introduction of new animals, changes in social groups, and/or incompatible associations can lead to aggression, injury, illness, and even death (McBride & Hebb, 1948; McBride & Kritzler, 1951; Caldwell et al., 1968; Caldwell & Caldwell, 1977; Erwin & Deni, 1979; Abbott et al., 1988; de Waal, 1989a; Sweeney, 1990; Samuels & Gifford, 1997; Evans, 2015). In odontocetes, symptoms of poor health are often hard to detect before disease is already seriously advanced. High rates of aggression have been reported as an indicator of social stress in captive odontocetes together with social isolation (excluded from/avoiding the group), inappetence, inactivity, and stereotypical behaviour (Galhardo

et al., 1996; Waples & Gales, 2002; Clegg et al., 2015), making it a potential animal-based parameter to assess welfare. Changes in agonistic behaviours and dominance hierarchies could be important factors to monitor in captive odontocete groups (McBride & Hebb, 1948; Tavolga, 1966; Tayler & Saayman, 1972; Samuels & Gifford, 1997; Waples & Gales, 2002). For the endangered EAFPs and critically endangered YFPs, captive breeding is a crucial goal that is still far from successful. Monitoring the groups better might help in understanding relationships between individuals and in detecting changes to promote suitable grouping and good welfare, finally increasing chances of breeding.

Conclusion and Recommendations

Monitoring the social behaviour of captive odontocetes can allow for early detection and management of potential social problems that may increase levels of social stress for vulnerable individuals. To this end, quantitative methods should be used to monitor rates of agonistic behaviours among captive dolphins and porpoises. We suggest daily monitoring of agonistic interactions to identify those that might potentially become harmful or threatening to the social group, or might compromise the welfare or health of individuals. Following Webster's (2005) triangulation principle, we suggest that daily records of agonistic behaviour could also be correlated to physiological measures such as food intake, changes in weight, and blood parameters where possible to provide a full picture of social dynamics, potential health risks, and the influence of social stress in the management of odontocete groups. Our study highlights that there are differences in agonistic behaviours and social dominance among captive odontocete species. We also describe agonistic behaviours in two species of FPs for the first time, which may be helpful for future studies and for caretakers to better monitor the behaviour of these species and individuals.

This study also introduces a new method for daily assessment of agonistic behaviours and dominance relationships that can be easily adapted to the range of facilities keeping odontocetes. Samuels & Gifford's (1997) method could be used for an initial assessment of dominance relationships for each pair of individuals and, after this first insight, the Elo-Rating Method could ease the detection of changes in dominance status. The time and duration of observation sessions can be tailored by each facility to suit their own schedule, and the collected data can be quickly analysed daily. When changes are noticed, individuals should be closely observed to determine whether they are changes indicative of declining health or social structure.

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