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The Dynamic of Aggression: How Individual and Group Factors Affect the Long-Term Interspecific Aggression Between Two Sympatric Species of Dolphin

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Abstract

Interspecific aggression, similar to intergroup conspecific aggression, has been observed in a variety of taxa. The dominant group or individual is determined by multiple aggressive events and can be influenced by the size, age, or group size of the participating individuals. Interspecific aggression between Atlantic bottlenose (*Tursiops truncatus*) and spotted (*Stenella frontalis*) dolphins, both resident and sympatric to Little Bahama Bank, the Bahamas has been consistently observed for over two decades. However, it is unclear whether one species is more dominant and little is known about the factors that influence the progression of aggression. For this study, underwater video recordings of 32 aggressive encounters composed of 451 aggressive behavioural events were analysed over a 12-yr period (1993–2004). These were used to describe the interspecific aggression observed and quantify which factors (the species and age class of the participants or the group size and behaviour of spotted dolphin groups) had the strongest impact on the progression and outcome of aggression. Over the long term, interspecific aggression was bidirectional with neither species being more dominant. During a single encounter, spotted dolphin group synchrony had the strongest impact on the dynamic of aggression, specifically impacting which group (1) initiated aggression, (2) the direction of aggression and (3) the occurrence of dynamic shifts or dominance reversals. This is the first study to quantify the dynamic of aggression for this population, to document bidirectional aggression and dynamic shifts during long-term interspecific aggression in free-ranging delphinids, and this study quantifies the role of synchrony during interspecific aggression using underwater observations.

Introduction

Interspecific aggression has been well studied in a variety of taxa, including fish (e.g. Muñoz & Motta 2000; DiPaola et al. 2012; Natsumeda et al. 2012), birds (e.g. Orians & Willson 1964; Olendorf et al. 2004; Consla & Mumme 2012) and numerous species of mammal (e.g. Rychlik & Zwolak 2006; May-Collado 2010; Suwanvecho & Brockelman 2012). Interspecific aggression, similar to conspecific aggression, can function as a means to compete for and obtain a limited resource (e.g. mates, space, food resources) or to establish and/or change a dominance hierarchy (Stensland et al. 2003; Cafazzo et al. 2010; Stumpf & Boesch 2010). Interspecific aggression can be between individuals from different species, between groups of different species (May-Collado 2010; Suwanvecho & Brockelman 2012) or take the form of mobbing behaviour where a group targets an individual from a different species (Olendorf et al. 2004; Consla & Mumme 2012).

Dominant status is determined by multiple aggressive events between the same individuals or groups of individuals. Many factors influence fighting ability, or which individuals or groups will be dominant during an aggressive encounter and over the long term (Parker 1974). The body size of the individuals participating can influence interspecific interactions at various levels of behaviour including its function and outcome. Individuals of different body sizes differ in their energy needs and aggression may result from increased resource competition (Basset & De Angelis 2007; e.g. parrotfishes (*Sparisoma* sp.): Muñoz & Motta 2000; jewel damselfish (*Plectroglyphidodon lacrymatus*): DiPaola et al. 2012; shrews, Rychlik & Zwolak 2006; and large mammals: Malinowski 2011; C. R. Malinowski & D. L. Herzing, own data). Exerting dominance or establishing and/or challenging an existing dominance hierarchy also result in aggression. Larger-sized individuals have been positively associated with dominant status and aggressive ability (Archer 1988). Larger-sized individuals are often observed performing aggressive behaviours and exerting dominance towards smaller-sized individuals (e.g. Archer 1988; Rychlik & Zwolak 2006; Cafazzo et al. 2010; May-Collado 2010). This could result in the harm, or even death, of the smaller-sized individuals (e.g. infanticide Patterson et al. 1998). In cases where individuals are of a similar size groups may be equally competitive, which could result in bidirectional aggression (e.g. gibbons (*Hylobates lar* and *H. pileatus*): Suwanvecho & Brockelman 2012). Sex can be indicative of which individuals participate in aggression and the function of aggression. Examples include mate competition where multiple males fight with females present (e.g. Japanese fluvial sculpin (*Cottus pollux*): Natsumeda et al. 2012) or males defending territory (e.g. in gibbons, Suwanvecho & Brockelman 2012). The age of the individuals participating can be indicative of which individuals hold a higher dominant status, which can be used to predict the direction of aggression and the behaviour of the individuals (e.g. domestic dogs *(Canis lupus familiaris)*: Cafazzo et al. 2010). Finally, the presence of a coalition or additional individuals can have a significant effect on which group is more dominant and the outcome of aggression. This has been observed in a range of animal taxa where coalitions and pair-bonds were crucial in enabling lower ranking individuals to obtain a higher dominant status, crucial in leading to dominance reversals and an important factor for a successful outcome (e.g. Herzing & Johnson 1997; Kitchen 2004; Kutsukake & Hasegawa 2005; Gagliardi-Seeley 2012).

Dominance hierarchies and an individual(s)' dominance status can depend on the group composition or context. These relationships, if formed, are not always stable. Status can change during a single aggressive encounter or over the long term through multiple interactions. Competition for a dominant status and dominance reversals, events where a subordinate individual becomes the dominant individual, have been observed in many taxa (e.g. fish Gagliardi-Seeley 2012; primates Kutsukake & Hasegawa 2005; and marine mammals Samuels & Gifford 1997). It is suggested for non-human animal conflict that dominance relationships between groups or individuals will be unstable when a dominance reversal is more likely to occur (i.e. more closely ranked individuals) (Johnson 1989). It follows that if two different species are similar in their dominance status relative to the other, the dominance relationship between the two species should be unstable, and thus, aggression likely to occur continuously over time (e.g. Kitchen et al. 2005; Rychlik & Zwolak 2006; Heitor & Vicente 2010).

In the Bahamas, the Atlantic spotted dolphin (*Stenella frontalis*) and the coastal ecotype of the Atlantic bottlenose dolphin (*Tursiops truncatus*) are resident, sympatric species to Little Bahamas Bank (referred to as LBB). Since 1985, these two species have been the focus of the Wild Dolphin Project's (WDP) long-term study. The bottlenose and spotted dolphins have been habituated to human presence in the water and the life history, social structure, behaviour and vocalizations of both species have been well described and studied (Herzing 1996, 1997; Herzing & Johnson 1997; Rossbach & Herzing 1997, 1999; Herzing et al. 2003; Miles & Herzing 2003; Rogers et al. 2004; Green et al. 2007; Malinowski 2011; Cusick 2012; Elliser & Herzing 2012, 2013a,b; Herzing & Elliser 2013; C. R. Malinowski & D. L. Herzing, own data).

Interspecific encounters, which make up 15 per cent of all the dolphin encounters observed on LBB have been documented consistently over the past 25 years (Herzing & Johnson 1997). Non-aggressive interspecific interactions range from affiliative (e.g. play) to foraging and travel (Herzing & Johnson 1997; Cusick 2012; Herzing & Elliser 2013; J. A. Cusick, own data). The group composition, number of individuals present, number of individuals interacting and individual/group behaviour change across behavioural contexts (Herzing & Johnson 1997) and can change multiple time during an interspecific encounter (e.g. Miles & Herzing 2003; Connor et al. 2011). On LBB, during non-aggressive interspecific encounters, spotted dolphins were typically observed in larger groups ($\bar{x} = 10.1$, range 1–40) compared to bottlenose dolphins ($\bar{x} = 4.4$, range 1–19) (Herzing & Johnson 1997; J. A. Cusick, own data).

Interspecific aggression, which makes up approx. 30% of all interspecific encounters, has been documented consistently over the past 25 years. Neither species has been displaced from the bank, as yearly field seasons have resulted in the same individuals being resighted and new calves continuing to be born for both species. The bottlenose and spotted dolphins differ in their group composition and overall behaviour during interspecific aggression. The overall group size of spotted dolphins tends to be larger than the group size of the bottlenose dolphins (Herzing & Johnson 1997; Herzing & Elliser 2013). Additionally, the average number of individuals participating in aggression is higher for spotted dolphins than for bottlenose dolphins (Herzing & Johnson 1997; Elliser 2010). Males of both species typically participate in the interspecific aggression, and females are present but mostly inactive (Herzing & Elliser 2013). For spotted dolphins, adults and in some cases juveniles participate in the interspecific aggression, whereas adult bottlenose dolphins participate in the aggression almost exclusively. Previous work suggested that during interspecific aggression, the presence and size of male spotted dolphin groups (referred to in this paper as 'spotted groups') were crucial in determining the outcome for spotted dolphins, whereas the presence of bottlenose dolphin groups was not an important factor (Herzing & Johnson 1997; Elliser 2010; Cusick 2012). Additionally, it has been suggested that bottlenose dolphins, which are significantly larger than the spotted dolphins, use their larger body size to physically dominate the smaller spotted dolphins (Herzing & Johnson 1997; Cusick 2012).

Previous work on this population has not revealed the primary function or cause of this interspecific aggression on LBB. To date, many aspects of the behaviour and the progression of the aggression were not quantified. To determine the function of the aggression between these two species, it is necessary to quantify the dynamic of aggression. Specifically, when interspecific aggression occurs, it is important to identify which individuals participate in the aggression and how often, whether one species is more dominant over the other (i.e. which species is the aggressor and victim more often) and how individual factors and group behaviour affect the progression and outcome of aggression. This study provides the necessary foundation for understanding the aggression between Atlantic spotted and bottlenose dolphins on LBB by quantifying the factors that influence the progression of aggression. The goals of this study were to examine the specific dynamics of interspecific aggression after interspecific aggression began. We (1) described and quantified the occurrence of interspecific aggression, (2) tested whether one species was more dominant than the other species and (3) once aggression began, tested which factors had the strongest influence on the progression and outcome of interspecific aggression. This study is the first to quantity the dynamic of aggression for this population and one of the first to quantify interspecific aggression between free-ranging dolphin species using underwater observations.

Methods

Study Site

The study area is located on the western edge of Little Bahama Bank (LBB) off of Grand Bahama Island in the Bahamas (26°42′N, 79°00′W to 27°15′N, 79°08′W). This area is composed of clear, shallow water with depths ranging from six to sixteen metres and an average visibility of up to 30 m. This study site is ideal for underwater observations of dolphin behaviour.

Study Population

The bottlenose dolphins range in size from 317.5 to 408 kg (700–900 lbs) and 3–4 m in length. This is significantly larger than the spotted dolphins, which range in size from 90 to 136 kg (200–300 pounds) and 2–3 m in length. Age classes for spotted dolphins (described Herzing 1997; modified from *S. attenuate* Perrin et al. 1987) were determined using individual identification, spotting patterns on the body and overall body coloration. These age classes are defined in four categories (two-tone, speckled, mottled and fused) due to the degree of spotting and age in years (described Herzing 1997). For this study, spotted dolphin age classes were combined into two categories: (1) juvenile (two-tone and speckled, ranging 1–8 yr) and (2) adult (mottled and fused, ranging 9+ yr). Age classes for bottlenose dolphin can be determined through individual identification and overall body size. For the current study, the age class of bottlenose dolphins was combined into two categories: (1) juvenile (body size no greater than half the adult size, ranging 1–8 yr) and (2) adult (full body size, ranging 9+ yr) (Rossbach & Herzing 1997, 1999; Gibson & Mann 2008). When possible, sex for both species was determined by opportunistic observation of the genital slit, individual identification and field observational notes for the encounters that were used in the analysis. These encounter notes were written at the time the encounter took place and identify the individuals that interacted during an encounter.

Data Collection in the Field

Dolphin surveys (conducted from 1985 to present) occurred daily between 07:00 and 19:00 from May to September on the R/V *Stenella* (20-m live-aboard power catamaran). Sighting and encounter data were collected as part of the long-term database. This included dolphin individual identification, environmental data, and behavioural observations and recordings. A dolphin encounter began when human underwater observation of the dolphins began and ended when human underwater observation of the dolphins ended. At the beginning of a dolphin encounter, data on GPS location, time of day, habitat, group size and composition, and behavioural context were collected. If bottlenose dolphins were present, dorsal fin photographs were taken from R/V *Stenella*, and body scars and dorsal fin photographs were used to individually identify the bottlenose dolphins. Human observers entered the water and underwater photographs and video recordings were taken to individual identify spotted and bottlenose dolphins. Behaviour and vocalizations from both species were documented and recorded using surface observations and underwater video recordings, which were collected using video cameras in underwater housing units with attached hydrophones (e.g. Sony CCDV9 8 mm, Yashica KXV1u Hi 8 mm, Sony XR 550). Behaviour was recorded continuously using ad-lib, focal sampling and behavioural event scanning methods (Altmann 1974). When interspecific aggression occurred, the group participating in the interspecific aggression was the subject of the focal follow, and focal sampling methods (Altmann 1974) were used to record the behaviour.

Behavioural Definitions

Defining interspecific aggression

An interspecific aggressive encounter (referred to as 'aggressive encounter') was defined as a dolphin encounter where members of both dolphin species were present and aggressive behaviours were observed and vocalizations heard. An aggressive encounter began when human observation of aggression began and ended when human observation of the aggression ended. An interspecific aggressive event (referred to as 'aggressive event') was defined as a single, aggressive behavioural event performed by members of one species towards members of the other species. An aggressive event was measured as a single point in time (Altmann 1974). An aggressive encounter was composed of multiple aggressive events within the period of human observation.

Defining the behaviours and context

An underwater, dynamic aggressive ethogram was developed which consisted of six behavioural categories (Table A1). Each category was composed of specific behaviours, which included open-mouth displays, biting, chasing and side mounting. Modifiers were used to further describe the behaviours observed (e.g. direction of behaviour, group size). This ethogram was used to score the behaviour that occurred at each aggressive event.

For each aggressive event (1), the size of male spotted dolphin groups, and if more than one spotted dolphin was present, (2) the behaviour of the male spotted group were scored. Figure 1a shows that the size of spotted dolphin groups consisted of three categories: (1) no group present, (2) association (1–3 male spotted dolphins) and (3) coalition (4+ spotted dolphins). If a male spotted group was present, the behaviour of the group was defined in terms of the behaviour of the individuals relative to one another. A group was either inactive (i.e. present, but not performing any aggressive behaviours) or the group was active. Figure 1b shows an active spotted group was either 'synchronous' or 'not synchronous'. A spotted group was synchronous meaning that individuals in the group performed the same behaviours in the same orientation at the same time relative to other members of the group. Alternatively, an active spotted group was 'not synchronous' meaning that individuals in the group performed similar or dissimilar behaviours at different orientations and at different times relative to other members in the group (i.e. coordinated). Multiple individuals could be in the area during an aggressive encounter; however, not all of these individuals were nearby or participating in the aggression. The male spotted dolphin group size and the behaviour of the group only referred to spotted dolphins that were present and near the aggression, observable in the video frame.

Defining the participants and the direction of aggression

For each single event in an aggressive encounter, the 'aggressor' was defined as the individual(s) that performed the aggressive behaviour. The 'victim' was defined as the individual(s) that received the aggressive behaviour. The 'initiator' of the aggressive encounter was defined as the individual(s) that performed the first aggressive behaviour (initiation event). Initiation was identified for each encounter when possible (see *video analysis procedure* section).

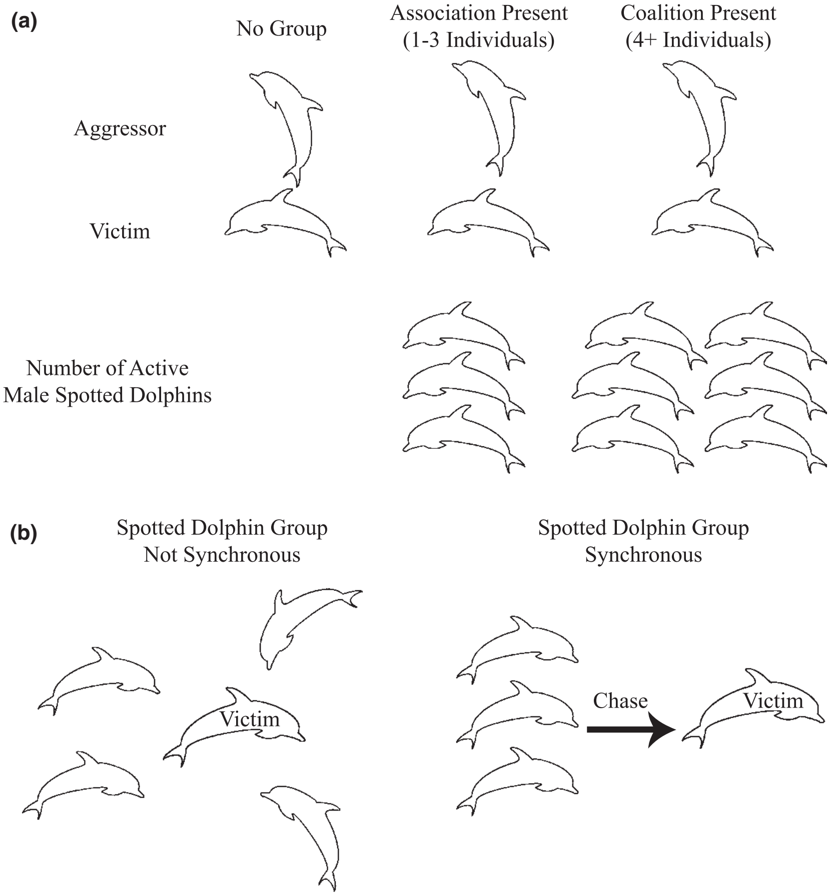

Fig. 1: The group size categories and behaviour of male spotted dolphin groups. Group size (a) was determined by the number of additional male spotted dolphins present. A male spotted dolphin group, regardless of size, could be either inactive or active. Inactive groups were present, but not performing any behaviours. An active male spotted dolphin group (b) was scored as either non-synchronous or synchronous.

Depending on the number of individuals participating, the 'aggressor', 'victim' and 'initiator' was a single individual or were multiple individuals. Regardless of the group size, the participants were scored as a single unit (e.g. aggressor), and the species, age class and the number of individuals performing the behaviours were noted.

During a single aggressive encounter, the direction of aggression was not always unidirectional or constant. During some encounters, the direction of aggression reversed. Members of the species that were the aggressor became the victim and the species that was the victim became the aggressor. This direction reversal was defined a 'dynamic shift' (Table A1): an event where the direction of aggression reversed. A dynamic shift occurred 'in favour of' the species that became the new aggressor. To score a dynamic shift, a sequence of two events needed to occur. The individual initially receiving aggression needed to perform two consecutive aggressive behaviours towards the initial aggressor (see Figure S1). The first behavioural event was defined as a reaction behaviour (Table A1). If the second aggressive behavioural event occurred, it was scored as a dynamic shift.

Video Recording Selection and Criteria for Analysis

Video recordings of dolphin encounters between the years of 1993 and 2004 were selected from the long-term database for analysis. By reviewing the video logs (detailed descriptions of observations within a video recording) and through preliminary observations of the video, we confirmed which video recordings contained interspecific aggressive encounters. From these known video recordings, interspecific aggressive encounters were randomly selected for analysis. Analysis was limited to video recordings that documented a minimum of three minutes of the aggressive encounter, which ensured adequate time for the dynamic of aggression to be observed (similar protocol: Miles & Herzing 2003; Melillo et al. 2009). Any video recording that did not meet these initial criteria, or upon further observation failed the meet the criteria, was not used in the analysis.

Video Analysis Procedure

Each video recording analysed contained a single aggressive encounter. All video recordings were viewed and scored using the behavioural analysis software program Observer XT 7.0 formatted for Windows. This allowed for behavioural coding and scoring with an ethogram and integrated video media (Noldus Information Technology 2011). Video scoring began when both species were observed in the video frame. Video scoring ended when (1) aggression between the two species ended and no aggression occurred for the remainder of the video recording, (2) when one or both species left the video frame and did not return for the remainder of the video recording or (3) when the video recording ended.

The initiator of an aggressive encounter (see *Defining the participants and direction of aggression section*) was determined only for video recordings that met the following criteria. At the beginning of the video recording, either (1) one species was present and the second species entered the video frame and no aggression was occurring or (2) both species were present in the video frame, but no aggression was occurring. The initiator was not scored if at the beginning of the video recording, both species were present and engaged in aggression, or if the video clarity was poor at the beginning of the video recording.

The outcome of the aggressive encounter was scored as observable or not observable. A video recording had an observable outcome if aggression ended, and (1) both species were present in the video frame or (2) one species left the video frame. The outcome was not observable if aggression continued and both species left view or the video recording ended.

Only individuals and behaviours fully observed within the video frame were scored. If all individuals were not visible in the video frame for a time period >5 s, this was noted and behavioural scoring stopped until individuals reappeared in the video frame (Altmann 1974; Dawkins 2007; similar protocol Nowacek 2002). This video analysis procedure provided the sequences of events for each aggressive encounter. When necessary sequences of events within an encounter were viewed multiple times at faster and slower play-speeds to ensure accurate scoring of individual and group behaviour.

Determining the Dominant Group and Victim for an Aggressive Encounter

For each aggressive encounter, the species that was dominant and victim was determined. The number of aggressive events that members of each species were the aggressor was used to determine which species dominated an aggressive encounter. If the aggressive encounter was unidirectional, the dominant species was considered the species that was the aggressor during the encounter. If the aggressive encounter was bidirectional (i.e. a dynamic shift occurred and members of both species were the aggressor for some of the aggressive events), then it was necessary to determine whether one species was dominant. A two-tailed chi-squared goodness-of-fit test with a Yates correction for continuity (e.g. Zar 1999) was conducted to determine whether members of one species were the aggressor for significantly more behavioural events than members of the other species. If a significant difference was detected, the species that was the aggressor for more behavioural events was considered dominant for that encounter. If no significant difference was detected, then a dominant group could not be determined for that encounter and was not used for those particular analyses. Similar protocol was used to determine which age class was dominant for each aggressive encounter and which species and age class were the victim for each encounter.

Determining the Factors that Affect the Progression and Outcome of Aggression

Once aggression began, the progression and outcome of aggression were measured at three levels: (1) the group that performed the first aggressive behaviour (i.e. initiated aggression), (2) the occurrence of a reaction behaviour and (3) the occurrence and direction of dynamic shifts. We determined whether individual factors of the participants (species or age class) or if group factors (spotted dolphin group size and behaviour) best predicted the onset and progression of aggression.

Statistical Analysis

Thirty-two aggressive encounters, composed of 451 aggressive events, met all the criteria necessary for video scoring and analysis. Nonparametric tests were used for all analyses due to the variable nature of the behaviours observed, most of the data were categorical and because the data did not meet the parametric assumptions of normality (Siegal & Castellan 1988). Two-tailed chi-squared goodness-of-fit test with a Yates correction for continuity (χ^2) and the log-likelihood ratio goodness-of-fit test (*G*-test) (Zar 1999) were used for the dominance data, initiation data, reaction behaviour data and dynamic shift data. In addition to the Yates correction, a modified Bonferroni test was conducted to account for multiple comparisons of similar data (Martin & Bateson 2007; similar protocol Kapheim et al. 2012). For the statistical analyses on dominance and the progression of aggression, three comparisons were made: between species, age class and group factors. The corrected alpha level after the Bonferroni test was alpha = 0.02 ($\alpha = 0.02$, e.g. see Martin & Bateson 2007). Any test that resulted in an alpha level >0.02 was considered non-significant (ns). All tests were conducted using the statistical software program R version 2.9.2 for MAC (The R Foundation for Statistical Computing ISBN 3-900051-07-0). To continue to ensure statistical validity, the more conservative results were reported for all analyses, and in cases where small frequency data were compared, only *G*-tests were reported (Zar 1999).

One primary observer, JAC, scored all videos. To ensure rater reliability, a second observer was trained to use the underwater ethogram, and twenty per cent of the aggressive encounters were randomly selected and scored in Observer XT 7.0 by the second rater (Martin & Bateson 2007; similar protocol Meunier et al. 2012). Rater reliability was calculated using Pearson's r correlation (r) and coefficient of determination (r^2) in R 2.9.2 for MAC. A significant correlation was determined as $r > 0.81$ ($\alpha = 0.05$) and $r^2 > 0.65$, which indicated a strong correlation (Gravetter & Wallnau 2004). Rater reliability results revealed that both raters were consistent and observations were highly correlated (for all tests: r (4)>0.90, $p < 0.05$ and $r^2 > 0.85$; see Table S1).

Results

Thirty-two aggressive encounters, composed of 451 aggressive events, were analysed for this study to determine once aggression occurred, which groups were more dominant and what factors influenced the progression of aggressive interactions. A total of 462.5 min of aggression were analysed ($\bar{x} \pm SE$ = 15 min ± 1.54, n = 32). The longest encounter was 43 min, and the shortest encounter was three minutes. For 28 of the 32 aggressive encounters, the species that dominated and the species that was the victim were identified. The remaining four encounters were considered bidirectional, meaning that a dominant group and victim could not be identified (i.e. the number of aggressive behavioural events each species was the aggressor and victim was not significantly different). For 24 encounters, the species that initiated aggression was identified.

Spotted dolphins dominated 16 encounters and were the victim for 12 encounters. Bottlenose dolphins dominated 12 encounters and were the victim for 16 encounters. Spotted dolphins initiated 15 aggressive encounters, and bottlenose dolphins initiated nine aggressive encounters. Twenty-seven dynamic shifts occurred (n = 12 aggressive encounters), which indicates that more than one dynamic shift occurred in some aggressive encounters. Thirteen dynamic shifts were in favour of spotted dolphins, and 14 dynamic shifts were in favour of bottlenose dolphins. Adults dominated 23 encounters (bottlenose = 11, spotted = 12), adults were the victim for 19 encounters (bottlenose = 14, spotted = 5), and adults initiated 23 encounters (bottlenose = 9, spotted = 14). Juveniles did not dominate any aggressive encounters, were the victim for five encounters (bottlenose = 0, spotted = 5) and initiated one encounter (bottlenose = 0, spotted = 1). Twenty-one dynamic shifts occurred in favour of adults (bottlenose = 14, spotted = 7), three occurred in favour of juveniles (bottlenose = 0, spotted = 3), and for three dynamic shifts in favour of spotted dolphins, the age category could not be clearly identified. Sixty-five reactions occurred, 41 were by bottlenose dolphins (adult = 41, juvenile = 0) and 24 were by spotted dolphins (adult = 12, juvenile = 12).

The Participants of Aggression: Species and Age Class

Adults, regardless of species, were involved in aggression significantly more often than juveniles. Adults were observed initiating aggressive encounters (chi-squared test with Yates correction: $\chi^2_1 = 20.17$, n = 24, p = 7.10E-06), dominating aggressive encounters (chi-squared test with Yates correction: $\chi^2_1 = 23.0$, n = 23, p = 1.62E-06) and were observed as the victim of aggressive encounters (chi-squared test with Yates correction: $\chi^2_1 = 8.17$, n = 24, p = 0.0043) significantly more often than juveniles. Dynamic shifts occurred in favour of adults significantly more often than juveniles (chi-squared test with Yates correction: $\chi^2_1 = 13.5$, n = 24, p = 0.00024).

The differences between the number of encounters initiated by bottlenose and spotted dolphins and the number of encounters each species dominated and was the victim were non-significant (for chi-squared results for this section, see Table 1). The difference between the number of encounters adult bottlenose and adult spotted dolphins initiated, dominated and were the victim was non-significant (Table 1). Juvenile spotted dolphins were the victim of some aggressive encounters, but were never observed dominating an aggressive encounter. Juvenile bottlenose dolphins were not observed participating in interspecific aggression. The number of dynamic shifts in favour of bottlenose and spotted dolphins occurred almost

Table 1: Results from the chi-squared test with Yates correction. All analyses were non-significant. The first and second set of analyses were conducted to compare the number of interspecific aggressive encounters each species and adult group initiated, dominated and was the victim. The third set of analyses were conducted to compare the number of dynamic shifts in favour of each species and in favour of each adult group

Test	n	χ^2	df	p (χ^2)
Encounter Initiated Bottlenose vs. Spotted Dolphins	24	1.50	1	0.22
Encounter Dominated Bottlenose vs. Spotted Dolphins	29	0.57	1	0.45
Encounters Victim Bottlenose vs. Spotted Dolphins	28	0.37	1	0.55
Encounter Initiated Adult Bottlenose vs. Adult Spotted Dolphins	23	1.09	1	0.30
Encounter Dominated Adult Bottlenose vs. Adult Spotted Dolphins	23	0.044	1	0.88
Encounter Victim Adult Bottlenose vs. Adult Spotted Dolphins	19	4.26	1	0.039
Dynamic Shifts Bottlenose vs. Spotted Dolphins	27	0.037	1	0.85
Dynamic Shift Adult Bottlenose vs. Adult Spotted Dolphins	21	2.33	1	0.13

'*'denotes significant difference at $p < 0.02$.

equally (differences were ns, Table 1). Similarly, dynamic shifts occurred almost equally for adult bottlenose and adult spotted dolphins (differences were ns, Table 1).

The Effect of Spotted Dolphin Groups – Size and Behaviour

Initiation was observed in 24 aggressive encounters (i.e. 24 initiation events). Spotted groups were present and synchronous for 13 initiation events (i.e. 13 encounters), and spotted groups were either not present or present/not synchronous for 11 initiation events (i.e. 11 encounters). The size of spotted groups also varied. Of the 24 aggressive encounters where initiation was observed, four encounters (i.e. four initiation events) were initiated when no spotted groups were present, seven were initiated when an association was present, and 13 encounters were initiated when a coalition was present. Spotted groups also changed in size and behaviour in the moments leading up to the initiation event. In 18 of the 24 encounters where initiation was observed, spotted group behaviour could be observed for up to one minute prior to the initiation event. In 11 of these 18 encounters, spotted group size or behaviour changed prior to the initiation event, and in seven encounters, spotted group size or behaviour did not change before the initiation event.

Of the 27 dynamic shifts observed, five occurred when no group was present, nine occurred when a spotted group was present but not synchronous, and nine occurred when a spotted group was present and synchronous. Of the 27 dynamics shifts observed, five occurred in the absence of spotted groups, 14 occurred when associations were present and eight occurred when coalitions were present.

Throughout aggressive encounters, spotted groups changed in size and behaviour. A total of 143 spotted group changes (size, behaviour or both) were observed ($\bar{x} \pm SE = 4.47 \pm 0.77$). The maximum number of group changes observed in a single encounter 21 and the lowest number of changes observed was zero (i.e. group size or behaviour did not change). During interspecific aggressive encounters ($n = 86$), the overall size of spotted dolphin groups present during aggression, although not necessarily participating in aggression, was larger ($\bar{x} \pm SE = 16.9 \pm 1.41$; range 2–69) compared to bottlenose dolphin groups that were present ($\bar{x} \pm SE = 5.3 \pm 0.32$, range 1–13). For comparison, we also observed during non-aggressive interspecific encounters ($n = 100$) that the overall number of spotted dolphins present, although not necessarily participating, ($\bar{x} \pm SE = 10.1 \pm 0.74$; range 1–40) was greater than that of bottlenose dolphins ($\bar{x} \pm SE = 4.4 \pm 0.39$; range 1–19).

Spotted Dolphin Behaviour

The behaviour of spotted groups had a significant effect on the progression of aggression for spotted dolphins. Figure 2a shows that when aggression began and was initiated by spotted dolphins, spotted groups were more likely to be synchronous (chi-squared test with Yates correction: $\chi^2_1 = 8.07$, $n = 15$, $p = 0.0045$). Additionally, Fig. 2b shows that when dynamic shifts in favour of spotted dolphins occurred spotted groups were more likely to be synchronous (goodness-of-fit test: $G_2 = 8.02$, $n = 13$, $p = 0.018$).

The group size of spotted dolphins also had an effect on the behaviour of participating spotted dolphins during aggression. Figure 3a shows that when aggression began and was initiated by spotted dolphins, larger spotted groups were more likely to be present (goodness-of-fit test: $G_1 = 13.45$, $n = 15$, $p = 0.00025$). The presence of spotted groups also had an effect on the occurrence and direction of dynamic shifts (Fig. 3b). Dynamic shifts that occurred in favour of spotted dolphins occurred significantly more often when a spotted group was present compared to when no group was present (goodness-of-fit test: $G_1 = 10.97$, $n = 13$, $p = 0.00093$).

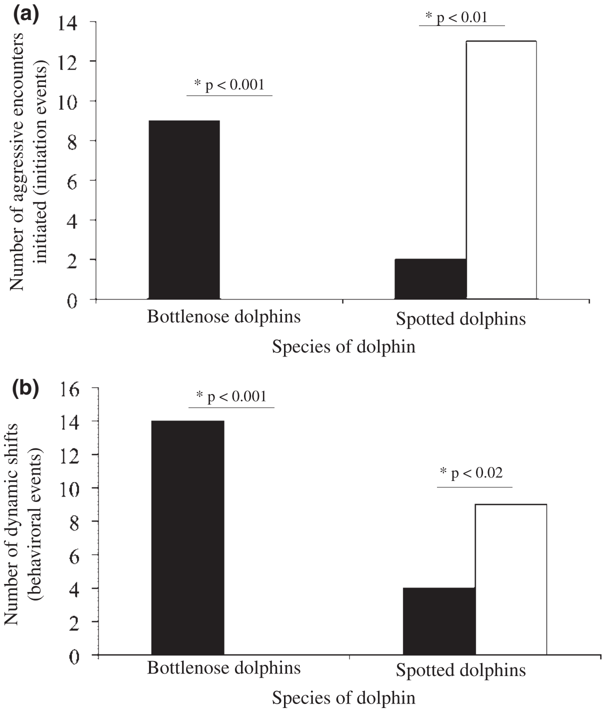

Fig. 2: The behaviour of male spotted dolphin groups when (a) bottlenose and spotted dolphins initiated aggression (performed the initiation event) and (b) when dynamic shifts occurred in favour of bottlenose and spotted dolphins. Black bars represent events where spotted groups were not present/present, but not synchronous. White bars represent events where spotted dolphin groups were present and synchronous. '*'denotes a significant difference (significance set at $p < 0.02$), and lines above bars represent compared groups. Initiation (n = 24 interspecific aggressive encounters) and dynamic shifts (n = 27 dynamic shifts) were scored as a single aggressive event.

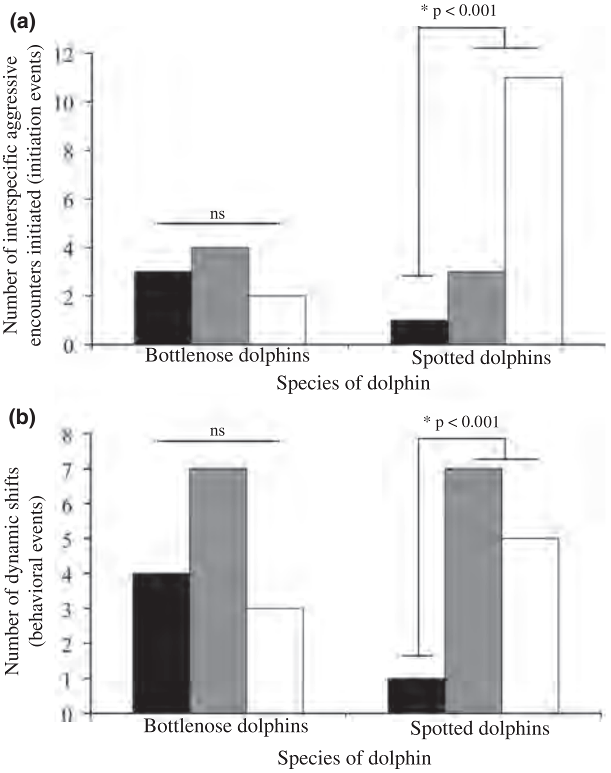

Fig. 3: The size of spotted dolphin groups when (a) bottlenose and spotted dolphins initiated aggression (performed the initiation event) and (b) when dynamic shifts occurred in favour of bottlenose and spotted dolphins. Black bars represent events where no spotted groups were present. Grey bars represent events where a spotted group association was present (1–3 individuals). White bars represent events where a spotted group coalition was present (4+ individuals). '*'denotes a significant difference (significance set at $p < 0.02$), and lines above bars represent compared groups. Initiation (n = 24 interspecific aggressive encounters) and dynamic shifts (n = 27 dynamic shifts) were scored as a single aggressive event.

Bottlenose Dolphin Behaviour

The behaviour of spotted groups had a significant effect on the behaviour of bottlenose dolphins. Figure 2a shows that of the nine observed initiation events performed by bottlenose dolphins, bottlenose dolphins were never observed initiating aggression when a spotted group was present and synchronous (goodness-of-fit test: $G_1 = 12.48$, n = 9, p = 0.00041). Additionally, of the 14 dynamics shifts in favour of bottlenose dolphins, none were observed when a spotted group was present and synchronous (Fig. 2b) and only occurred when a spotted group was not present or present, but not synchronous (chi-squared test with Yates correction: $\chi^2_1 = 14.0$, n = 14, p = 0.00018). Finally, bottlenose dolphins were observed performing 41 reaction behaviours. These reaction behaviours occurred significantly more often when no spotted group was present or spotted groups were present/not synchronous (n = 29) compared to when a spotted group was present and synchronous (n = 12) (chi-squared test with Yates correction: $\chi^2_1 = 7.05$, n = 41, p = 0.0079).

Spotted dolphin group size did not have a significant effect on bottlenose dolphins' behaviour during aggression. As shown in Fig. 3a, when aggression began and was initiated by bottlenose dolphins, there was no significant difference between the number of bottlenose initiation events and the size of spotted groups present (goodness-of-fit test: $G_2 = 0.68$, n = 9, p = 0.71). As shown in Fig. 3b, the number of dynamic shifts in favour of bottlenose dolphins that occurred when no spotted group was present, an association, and/or a coalition was present did not differ significantly (goodness-of-fit test: $G_2 = 1.79$, n = 14, p = 0.41). The number of reaction behaviours performed by bottlenose dolphins in the absence of spotted groups (n = 9), when associations were present (n = 16), when coalitions were present (n = 16), did not differ significantly (chi-squared test with Yates correction: $\chi^2_2 = 2.39$, n = 41, p = 0.30).

Discussion

Over the long term, interspecific aggression between the bottlenose and spotted dolphins on LBB was not unidirectional. When only considering a single aggressive encounter, members of one species, almost always adults, were identified as dominant by acting as the aggressor over multiple consecutive aggressive events. However, when considering the aggressive encounters collectively over the long term, both bottlenose and spotted dolphin groups dominated aggressive encounters and groups from both species were the victim of aggressive encounters. Collectively, these results suggest that one species was not more dominant than the other species and that during a single aggressive encounter, dominance between adult participants was dependent on the presence and behaviour of spotted dolphin groups. This is the first study to clearly quantify bidirectional long-term interspecific aggression in free-ranging delphinids using underwater observations.

The Direction of Aggression and Dominance

It is apparent from the data presented here that members of one species did dominate a single aggressive encounter. However, neither species dominated significantly more aggressive encounters than the other species revealing that over the long-term aggression between these two species was bidirectional. The occurrence of dynamic shifts revealed that a single aggressive encounter could be bidirectional and that being dominant at the onset of an aggressive encounter did not always result in being dominant throughout the aggressive encounter. An extreme example were the four bidirectional aggressive encounters where neither species could be identified as more dominant. Short- and long-term bidirectional aggression is unique to LBB because almost all other accounts of long-term interspecific aggression in delphinids have either documented unidirectional aggression or did not show behaviours indicative of aggression reversals, dynamic shifts or bi-directionality (Samuels & Gifford 1997; Frantzis & Herzing 2002; Psarakos et al. 2003; Wedekin et al. 2004; Acevedo-Gutiérrez et al. 2005; Quérouil et al. 2008; May-Collado 2010). Unidirectional interactions observed in other populations are used as an indicator of dominance (e.g. Hausfater 1975; Stensland et al. 2003; convict cichlid (*Amatitlania nigrofasciata*): Gagliardi-Seeley 2012). Similar to what was observed during most interspecific aggressive encounters on LBB, dominance status of an individual or group of convict cichlids was dependent on multiple consecutive aggressive behaviours that resulted in a favourable outcome (Gagliardi-Seeley 2012). On LBB, bidirectional aggression was observed because aggressive behaviours were displayed in equal number by both groups involved and aggressive encounters resulted in favourable outcomes for both groups over time. This has also been observed during interspecific interactions between gibbons (Suwanvecho & Brockelman 2012). Dominance in this bidirectional aggression was not determined by individual factors, which are more stable (i.e. age class or species of participants). On LBB, the dominant group was determined by contextual factors that changed both during a single encounter and from one encounter to the next, (i.e. location of aggression, group composition, size and/or behaviour) (e.g. chacma baboons (*Papio ursinus*): Kitchen et al. 2005; shrews: Rychlik & Zwolak 2006; Sorraia horses (*Equus caballus*): Heitor & Vicente 2010).

Factors Influencing the Progression and Outcome of Aggression

Synchronous behaviour, unique to spotted dolphin groups during interspecific aggression, had the strongest effect on the dynamic of aggression. The effect of synchronous spotted groups was observed at three different levels of behaviour for both species: initiation, dynamic shifts and reaction behaviours. Overall, once aggression began, spotted dolphins participating in aggression were more successful against bottlenose dolphins when spotted groups were synchronous; whereas bottlenose dolphins' behaviour was negatively impacted when spotted groups were synchronous. Mobbing behaviour, which is observed in many avian species, has a similar effect when multiple individuals chase after a potential predator as a single, often synchronous unit (e.g. red-winged blackbirds (*Agelaius phoeniceus*): Olendorf et al. 2004; Consla & Mumme 2012). During aggression, bottlenose dolphins, like the predators targeted by mobbing behaviour (Olendorf et al. 2004; Consla & Mumme 2012), modified their behaviour when synchronous spotted groups were present. Spotted dolphins' behaviour was also different in the context of synchronous spotted groups. When spotted dolphins initiated aggression, more often it occurred when spotted groups were synchronous. Furthermore, when spotted dolphins became the aggressor (i.e. dynamic shift), this occurred more often when spotted groups were synchronous. When bottlenose dolphins were observed initiating aggression, it never occurred when spotted groups were synchronous. Of the 14 dynamic shifts in favour of bottlenose dolphins, none occurred when spotted groups were synchronous and bottlenose dolphin attempted to become the aggressor (i.e. reaction behaviour) more often when spotted groups were not present or present, but not synchronous. Bottlenose and spotted dolphins appeared to weigh their 'power status' relative to one another during aggression, similar to other mammals (e.g. Japanese macaques (*Macaca fuscata*): Kutsukake & Hasegawa 2005) and modified their behaviour under these different contexts.

Group synchrony in spotted dolphins represents a form of cooperation between individuals (Noe 2006; Drea & Carter 2009). Cooperation can be of particular importance during aggression between different sized individuals, as it may allow smaller-sized, cooperating individuals, to overcome the inherent advantages of a larger-sized opponent (Archer 1988). Bottlenose dolphins, which are significantly larger than spotted dolphins, use sexual behaviours and their physical size to physically dominate the spotted dolphins (Cusick 2012; J. A. Cusick & D. L. Herzing, own data; Herzing & Elliser 2013). Analyses of behavioural events during interspecific aggression have revealed that side mounting, a sexual behaviour, was unidirectional performed by bottlenose dolphins onto spotted dolphins (Cusick 2012; J. A. Cusick & D. L. Herzing, own data). This unidirectionality was further supported by comparisons of sexual behaviours observed at the encounter level (Herzing & Elliser 2013). Group synchronization during interspecific aggression appeared to be unidirectional observed by spotted dolphins groups towards bottlenose dolphins (Cusick 2012; J. A. Cusick & D. L. Herzing, own data). When synchronous, the power of spotted groups, viewed as a single unit, was greater than an individual acting alone or different from the group. Therefore, a single bottlenose dolphin experienced the effect of the summation of multiple individual spotted dolphins, similar to the result of mobbing behaviour (Olendorf et al. 2004). The synchronization of spotted groups may serve as the spotted dolphins' method of overcoming the advantages of a larger-sized opponent and thus allow the spotted dolphins to dominate bottlenose dolphins.

The negative impact of spotted group synchrony on bottlenose dolphins' behaviour was not a function of spotted group size alone. In previous studies, it has been suggested that large coalitions of spotted dolphins (i.e. six spotted dolphins) performed chasing behaviour towards a single bottlenose dolphin (Herzing & Johnson 1997). The data presented here suggest a benefit of larger spotted groups, but also demonstrate that synchronous associations were as successful as larger, synchronous coalitions. When outnumbered only, bottlenose dolphins did not always respond submissively or alter their behaviour in response to larger spotted groups, as opposed to other mammalian species where individuals changed their behavioural response if they had the numerical advantage (e.g. Wilson et al. 2001; Kitchen 2004). Bottlenose dolphins were observed initiating aggression, performed reaction behaviours and dynamic shifts were still observed regardless of spotted dolphin group size. When spotted dolphins did initiate aggression and when dynamic shifts occurred, they occurred more often when a larger spotted group was present, which has been also observed in a variety of taxa (e.g. Goodall et al. 1979 & Goodall 1986 as cited by Watts 2004; Wilson et al. 2001; Watts et al. 2006; Mosser & Packer 2009; Talebi et al. 2009; Consla & Mumme 2012; Gagliardi-Seeley 2012). During aggression, non-synchronous spotted groups performed behaviours in a way that is described as coordinated in other animal groups: performing different behaviours or similar behaviours at different times (Noe 2006; Drea & Carter 2009). This coordinated spotted group behaviour did not have an effect on the dynamic of aggression. In accounts of aggression in primates (Boesch 2002; Watts et al. 2006; Talebi et al. 2009), lions (*Panthera leo)* (Mosser & Packer 2009) and wolves (*Canis lupis*) (MacNulty et al. 2007), a coordinated group was the critical factor in determining the positive outcome for the coordinating group and the negative outcome for the group that received the aggression. The effect of non-synchronous spotted groups on the behaviour of bottlenose and spotted dolphins was not significantly different from the effect of inactive spotted groups or when spotted groups were absent (Cusick 2012; J. A. Cusick, own data).

Group Behaviour Across Behavioural Contexts

This study has shown that the presence and behaviour of spotted groups had the strongest impact on the dynamic of aggression. In addition, it is apparent that the function of synchronous group behaviour for spotted dolphin during interspecific aggression was a means to dominate a larger-sized opponent. The current study has also shown that group size and behaviour can change during a single encounter multiple times and can vary across encounters. Even before the initiation event, spotted group size and behaviour sometimes changed, including becoming larger and synchronous, or dissipating and/or becoming non-synchronous before the initiation event. Group size and behaviour can also vary between interspecific behavioural contexts, specifically non-aggressive encounters, which have been well described by Herzing & Johnson (1997). On LBB, interspecific encounters on average are larger than intraspecific encounters (Herzing & Johnson 1997). Our results also show that spotted dolphin groups that are present are often larger in size compared to bottlenose dolphin groups that are present both in non-aggressive interspecific interactions and aggressive interactions. Similarly, the size of groups participating in interspecific interactions differs, with spotted dolphins usually outnumbering bottlenose dolphins for a majority of the aggressive encounter (J. A. Cusick, own data). One important difference to note is bottlenose dolphins also form strong intraspecific alliances, which have been observed during bottlenose dolphin intraspecific interactions (Rogers et al. 2004; Elliser 2010), but not observed during interspecific aggression, which is discussed in greater detail in the following sections.

Spotted dolphins on LBB live in fission–fusion societies (Elliser & Herzing 2012, 2013a) meaning that members of social networks and all individuals within a given population are not necessarily present together at the same time (e.g. bottlenose dolphins: Connor et al. 2000). Therefore, it is not surprising that group sizes (and behaviour) change so frequently within a behavioural encounter and also between encounters. Group sizes changed relatively frequently during interspecific encounters on LBB, which was also observed in Shark Bay where the size of social alliance groups changed multiple times and quickly during intraspecific aggression for access to mates, in some cases increasing by four to six individuals in a matter of minutes (Connor et al. 2011).

Synchronous behaviour has been observed during foraging events (e.g. Bel'kovich 1991; coordinated hunting: Saayman et al. 1973), between mom/calf pairs (e.g. synchronous swimming, surfacing, breathing: Mann & Smuts 1999; Fellner et al. 2012) during play (Bel'kovich 1991) and between alliances during competition for mates (e.g. synchronous breathing and surfacing: Connor et al. 2006). Synchronous breathing and surfacing has been observed between individuals during travelling and social events (e.g. Sakai et al. 2010), and dive synchrony observed in whales (e.g. Whitehead 1996). On LBB both spotted and bottlenose dolphin groups have been observed performing synchronous behaviour during intraspecific interactions (e.g. mom/calf pairs: Miles & Herzing 2003; travelling, surfacing) and during non-aggressive interspecific interactions, albeit synchrony is not necessarily directional towards the other species, which is observed during interspecific aggression (Herzing & Johnson 1997; J. A. Cusick, own data). In addition, examples of interspecific coalitions have been documented where synchronous swimming and surfacing behaviour were observed and in some cases directed at a targeted individual (Herzing & Johnson 1997). The occurrence and duration of synchronous behaviour can change multiple times throughout a single encounter, across multiple encounters and differ depending on the behavioural context and group composition (e.g. Connor et al. 2006; Sakai et al. 2010; Fellner et al. 2012). In addition, the behavioural contexts associated with non-aggressive and aggressive interspecific interactions vary greatly (e.g. non-aggression/foraging vs. aggression/foraging; non-aggression/travel vs. aggression/travel: Cusick 2012). This reveals the complexity of these interactions and the function of behaviours used during the interactions. The broad use and yet subtle differences of synchronous behaviour in dolphin interactions suggests that synchrony may function differently depending on the group composition and behavioural context. The current study quantifies the dynamic of interspecific aggression, the function of synchronous group behaviour during interspecific aggressive interactions and reveals the benefit of synchronous behaviour for smaller-sized individuals against larger-sized individuals.

The Function of Interspecific Aggression

On LBB, interspecific aggression has been observed consistently for almost three decades, and neither species has been displaced. The aggression observed likely resulted from a combination of factors that changed depending on the time, location and context. Aggression was often between males of both species, and females were present, but inactive (Herzing & Elliser 2013). Therefore, the reason for the interspecific aggression on LBB could be defence against interspecific copulation (e.g. hybrid observation: Herzing et al. 2003; Elliser 2010; Cusick 2012), similar to the mate defence observed during conspecific intergroup aggression in male bottlenose dolphins (Connor et al. 1992, 2006) and spider monkeys (*Ateles geoffroyi*) (Campbell 2006). For spotted dolphins, participating in aggression and coalition membership could have an intraspecies fitness benefit similar to that observed in chimpanzees (*Pan troglodytes*) (Gilby et al. 2013) and black grouse (*Tetrao tetrix*) (Hämäläinen et al.

2012) where participating individuals may increase their chance of siring offspring. It is unlikely that aggression resulted primarily from habitat and food competition because Malinowski (2011) found that the bottlenose and spotted dolphins on LBB foraged in significantly different habitats, on significantly different prey items, at different times of the day, and on different areas of the bank (C. R. Malinowski & D. L. Herzing, own data). However, aggression could be used to maintain this niche segregation (Malinowski 2011; C. R. Malinowski & D. L. Herzing, own data). Alternatively, aggression has been observed between groups of chimpanzees as a means to defend their territory (Watts et al. 2006). Groups patrol and crossover specific boundary lines (Watts et al. 2006), but on LBB, similar behaviour and the locations of aggression did not reveal patterns indicative of territorial boundaries (Cusick 2012). Additional work is needed to identify to what degree these factors lead to interspecific aggression and if aggression differs under these varying contexts.

Future work should also address what influenced the spotted dolphins' decision to participate in aggression (e.g. Kitchen & Beehner 2007) and why individual spotted dolphins formed groups and synchronized during some aggressive encounters, but did not form groups or failed to synchronize their behaviour during other encounters. Individuals may be more likely to participate in aggression or change their behavioural strategy if there is a numerical advantage in their favour (e.g. McComb et al. 1994; Kitchen 2004; Nieh et al. 2005; Vogel et al. 2007; Meunier et al. 2012). Adult male spotted dolphins form strong, and in many cases, life-long alliances with other adult males (Elliser & Herzing 2013a,b), which come together during interspecific aggression to form the larger, temporary coalitions. It is possible that strongly aligned individuals are more likely to form synchronous groups (e.g. primates: Watts 2004; dolphins: Connor et al. 2006) if other individuals in their alliance are the target of aggression. Additional work is necessary to examine the individual composition of spotted groups and their alliance strength to determine whether there is a relationship between the synchronous groups and/or the victim of the aggression.

Secondly, intraspecies groups were not an important factor for bottlenose dolphins during aggression (Herzing & Johnson 1997; Elliser 2010; Cusick 2012; J. A. Cusick & D. L. Herzing, own data), and synchronous group behaviour appeared to be a unidirectional behaviour performed only by spotted dolphins towards bottlenose dolphins. It is necessary to determine how the unidirectional side mounting behaviour and the other behaviours observed affect the dynamic of aggression. Additionally, it is necessary to examine why juvenile spotted dolphins were observed participating in aggression, but juvenile bottlenose were not observed. Finally, additional study is necessary to examine the intraspecies social dynamics of bottlenose dolphins that may influence which bottlenose dolphins participate and why larger groups of bottlenose dolphins were not observed during aggression (Elliser 2010).

Comparing the behaviour of bottlenose and spotted dolphin during aggressive encounters to behaviour observed during non-aggressive interspecific encounters was beyond the scope of this study. Broadly speaking, there are many similarities between aggressive and non-aggressive interspecific encounters (e.g. spotted dolphins tend to outnumber bottlenose dolphins, synchronous group behaviour is observed). But, there are clearly many differences between aggressive and non-aggressive encounters, which include more noticeable differences like group composition and group size of present and/or interacting individuals (e.g. adults vs. juveniles, males vs. females, group size differences) and more subtle differences (e.g. directionality of behaviour including synchronous behaviour). Future work should quantify the synchronous behaviour of both spotted and bottlenose dolphin groups during non-aggressive interspecific interactions as well as aggressive intraspecific interactions. This would provide additional insight into the function of synchronous behaviour for delphinids during aggressive and non-aggressive interactions.

Conclusion

These results demonstrate that aggression between bottlenose and spotted dolphins was bidirectional over the long term, with adult groups of both species successfully dominating multiple encounters. During a single aggressive encounter dominance, the direction of aggression, and the dynamic of aggression were most strongly impacted by the synchronous behaviour of spotted groups and not the spotted dolphin group size or the species of the participants. This study is the first to quantify the dynamic of aggression for this population and, to our knowledge, the first to reveal clear, long-term bidirectional interspecific aggression and dynamic reversals in delphinids using underwater observations of behaviours. This study provides an important marine example of the benefits of group behaviour during interspecific aggression and more importantly the importance of synchronous groups vs. coordinated groups or inactive groups. This marine example is very similar to avian mobbing behaviour and is comparable to the coordinated group behaviour observed during many interspecific and intergroup conflicts between varieties of terrestrial taxa. This study demonstrates the complexity of aggressive interactions, the need to examine the influence of multiple contextual factors, and the importance of examining the way these factors interact and change over time to quantify the dynamic of aggression.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1: The necessary sequence of events to observe a reaction behaviour and a dynamic shifts.

Table S1: Rater reliability for interspecific aggressive encounters.

Appendix

Table A1: Underwater interspecific aggressive dynamic ethogram. This ethogram consists of six behavioural categories, which are composed of multiple behaviours. This ethogram was used to score each interspecific aggressive behavioural event during an interspecific aggressive encounter. A dynamic shift and reaction behaviour are represented by category six

Behavioural category	Behaviour	Description
(1) Visual		Actions that are visually displayed, no contact is made between individuals
	Open Mouth	Dolphin or group opens mouth towards another dolphin or group of dolphins
	Jaw Snap	Dolphin open and shut jaw rapidly, direct to dolphin
	Body Jerks	Dolphin moves head or body in erratic or rapid motion
	Displays	Dolphin arches/contorts body in the water column, stationary
(2) Contact		Actions/behaviours that result in physical contact or touching between individuals
	Tail Contact	One dolphin or group swipes or makes contact with another dolphin or group using tail
	Body, rostrum, pec contact	One dolphin makes contact with another dolphin or group, usually in aggressive context with body, rostrum or pectoral fin
	Bite	One dolphin bites or rakes another dolphin on body or tail
	Head to Head	Dolphin or group takes head-to-head position with another individual or group
(3) Pursuit		Actions that involve individuals following or moving after other individuals
	Chase	One or group of dolphin chases another individual or group in fast, medium or slow chase
	Charge	Two or more dolphins charge each other in head-to-head format, sometimes making contact
	Follow	An individual or group swims alongside or behind another individual or group in the same direction or path
(4) Sexual Displays		Behaviours that are related or used during sexual behaviour
	Erection	Penis is visible outside genital slit. No contact with other dolphins and no other behaviours occurring
	Side Mount	One or more dolphins side mounts or rubs genitals against another individual(s)
(5) Changes in Group	Change Group Composition	Change in the age class of group members
	Change Group Size	Change in the number of individuals in the group
(6) Dynamic Shift		Event in which the species/age class that was the initial victim becomes the aggressor and the species/age class that was the initial aggressor becomes the victim
	Reaction	First aggressive behaviour in a sequence of two performed by the initial victim towards the initial aggressor. A second aggressive behaviour in sequence is scored as a dynamic shift