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Affiliative Behavior After Aggressions in Common Bottlenose Dolphins (*Tursiops truncatus*)

Chisato Yamamoto[1, 2] and Nobuyuki Kashiwagi[3]

[1]*Cetacean Research Center, Graduate School of Bioresources, Mie University,*
1577 Kurimachiya-cho, Tsu, Mie 514-8507, Japan
[2]*Faculty of Life Science and Biotechnology, Fukuyama University, 985-1 Fukuyama, Hiroshima 729-0292, Japan*
E-mail: chisato.yamamoto14@gmail.com
[3]*Kagoshima City Aquarium, 3-1 Honkoushinmachi, Kagoshima 892-0814, Japan*

Abstract

Affiliative behavior in social animals may have several functions such as maintaining social bonds, reducing tensions, or restoring relationships. Common bottlenose dolphins (*Tursiops truncatus*) engage in several affiliative behaviors, including parallel swimming, contact swimming, and flipper rubbing. Dolphins affiliate with former opponents after aggression, suggesting that this is a function of tension reduction. This study investigated how affiliative behaviors occur after aggression. Parallel swimming occurred more frequently than expected after aggression, while contact swimming and flipper rubbing occurred less frequently than expected. Parallel swimming and contact swimming occurred immediately after aggression; in contrast, flipper rubbing tended to occur more than one minute after aggression. These results suggest that common bottlenose dolphins engage in parallel swimming and contact swimming when social tension increases. The function may differ among these affiliative behaviors, and dolphins may engage in specific affiliations after aggression.

Key Words: affiliative behavior, aggression, parallel swimming, common bottlenose dolphin, *Tursiops truncatus*

Introduction

Many social animals show affiliative interactions through contact or proximity (Dunbar, 1991; Hart & Hart, 1992; Kutsukake & Clutton-Brock, 2006; Radford & Du Plessis, 2006; Matoba et al., 2013). Affiliative behaviors may be used in several contexts, including to maintain social bonds, to reduce social tension after aggression or reunions, to restore affiliative relationships after aggression, or to trade for commodities such as infant handling or shared feeding tolerance (Aureli & van Schaik, 1991; Fraser et al., 2008; Palagi et al., 2008; Kutsukake & Clutton-Brock, 2010; Matoba et al., 2013). Some animals may use affiliative behaviors in differing contexts between aggressive and non-aggressive situations (Kuroda, 1980; de Waal & Yoshihara, 1983; Call et al., 2002; Kutsukake & Castles, 2004; Seed et al., 2007). For example, chimpanzees (*Pan troglodytes*) perform many affiliative behaviors, including kissing, grooming, embracing, and gentle touching (Kutsukake & Castles, 2004; Fraser & Aureli, 2008; Romero & de Waal, 2011). Kissing and gentle touching occur more frequently after aggression, while grooming and embracing usually occur in non-post-conflict situations (Kutsukake & Castles, 2004; Romero & de Waal, 2011). Rhesus monkeys (*Macaca mulatta*) perform several affiliative behaviors, including grooming, embracing, lip-smacking, and teeth-baring. Embracing and lip-smacking often occur after aggression rather than in non-post-conflict situations, while grooming is common in non-post-conflict situations (de Waal & Yoshihara, 1983; Maestripieri & Wallen, 1997). In non-primate species, rooks (*Corvus frugilegus*) engage in several affiliative behaviors, including bill-twining, preening, displaying, and food sharing. However, bill-twining and displaying occur more frequently after aggression than after non-aggressive activities (Seed et al., 2007).

Common bottlenose dolphins (*Tursiops truncatus*) live in a fission–fusion society where group membership often changes (Wells et al., 1987; Connor & Wells, 2000). Adult females have many social relationships and relatively strong bonds with specific females (Wells, 1991; Lusseau et al., 2003). Calves maintain a strong bond with their mothers until weaning at between 3 and 6 y old (Wells, 1991; Grellier et al., 2003; McHugh et al., 2011). Bottlenose dolphins have several affiliative behaviors that may have contrasting functions. Parallel swimming is a synchronous behavior in which two or more dolphins swim close to each other and may function as a signal to reduce tension or represent a signal of cooperation between allied males (Connor et al., 2006; Sakai et al., 2010); contact swimming is a behavior in which one dolphin touches another dolphin's body via the pectoral fin, and it may reduce the stress of females who receive harassment by males (Connor et al., 2006); and flipper rubbing is a contact behavior in which one individual rubs the body of another via its pectoral fin (Sakai et al., 2006). Flipper rubbing may reduce tension after aggression or social bonding within same-sex, same-aged pairs, especially among males (Tamaki et al., 2006; Dudzinski & Ribic, 2017).

Common bottlenose dolphins exchange affiliative behaviors after aggression (Weaver, 2003; Holobinko & Waring, 2010; Yamamoto et al., 2015). It has been suggested in previous studies that social tension reduces when former opponents engage in affiliation with the opponents or bystanders (Yamamoto et al., 2015). However, it is unclear how three affiliative behaviors—parallel swimming, contact swimming, and flipper rubbing—occur after aggression. If affiliative behaviors have contrasting functions, common bottlenose dolphins should engage in affiliations that function in tension reduction after aggression. In addition, if the functions differ as to whether the dolphin is touched via the pectoral fin, the frequency of the act should vary according to the actor's position (the aggressor, the recipient of aggression, or the bystander). This study investigated how common bottlenose dolphins use these affiliative behaviors after aggression.

Methods

Study and Subjects

Five adult female bottlenose dolphins and three calves were observed in the Kagoshima City Aquarium in Japan. The three calves (one male and two females) were born in 2012, 2013, and 2016, respectively. All observations and video recordings (Marine Eye; KOWA Co., Ltd, Marine System Department, Osaka, Japan) were made through an underwater window at the main pool (16 m long, 10 m wide, and 5.5 m deep). Individuals in the main pool changed during the study period because members were shifted with dolphins in the other pool.

Data Collection

Data collection was conducted for 90 d between August 2012 and February 2015 and for 55 d between April 2017 and October 2018. Chasing, hitting, and biting are considered aggressive behaviors (Samuels & Gifford, 1997; Holobinko & Waring, 2010; Yamamoto et al., 2015; Serres et al., 2019). Chasing was defined as one dolphin pursuing another individual at a fast speed; hitting was defined as one individual making violent contact with another dolphin using its head, tail, or body; and biting was defined as a dolphin making violent contact with another dolphin using its teeth. The end of the aggressive event was defined as the time when both dolphins stopped chasing, biting, and/or hitting. However, if the same pair restarted an aggressive exchange within 1 min, we decided that the previous aggression was still going on. Aggressions between two individuals were recorded. A dolphin who dealt with an aggressive encounter was defined as a former opponent, and individuals who did not engage in the aggression but were in the same pool were defined as bystanders. Infants (under 1 y old) were not included in the former opponent and bystander interactions. The former opponent was classified as an aggressor and a recipient of aggression. As counterattacks occurred during a single aggression, the aggressor was defined as the individual who attacked the opponent at the end of the aggression, and the recipient of aggression was the other individual.

The post-conflict (PC) period was set at 10 min after aggression based on previous studies (de Waal & Yoshihara, 1983; Yamamoto et al., 2015). We collected only one datum from each pair in each period between feeding events. We recorded whether the former opponent engaged in parallel swimming, contact swimming, or flipper rubbing in the PC period. When an affiliative behavior occurred, the individual IDs of the common bottlenose dolphins that engaged in affiliative behavior were recorded. When different affiliative behaviors occurred in the same PC period, we recorded all affiliative behaviors (e.g., when contact swimming and flipper rubbing occurred in the same PC, we recorded both affiliative behaviors). The affiliative behaviors included parallel swimming, contact swimming, and flipper rubbing (Sakai et al., 2013). Parallel swimming was defined as when two dolphins had close proximity (< 0.6 m) and swam in the same direction and at the same speed (Sakai et al., 2010, 2013) but did not touch or rub each other; contact swimming was defined as when two dolphins swam side by side and one dolphin placed its pectoral fin against the side of the second individual (Connor et al., 2006); and flipper rubbing was defined as two dolphins swimming together, where one dolphin came into contact with the other via its pectoral fin and either or both dolphins moved their touching body parts, including their pectoral fins or bodies (Sakai et al., 2006). When contact swimming occurred, we recorded the actor who touched the other via its pectoral fin. Contact swimming was recorded once per pair per PC period (e.g., when not only the aggressor but also the recipient of aggression performed contact swimming with bystanders, we recorded the actor of both contact swimming between the aggressor and the bystander, and between the recipients of aggression and the bystander). We recorded the latency from the end of aggression to the first occurrence of each affiliative behavior.

Statistical Analyses

We compared the number of PC periods in which parallel swimming occurred, the number of PC periods in which contact swimming occurred, and the number of PC periods in which flipper rubbing occurred using Fisher's exact test to investigate the type of affiliative behaviors that occur most often during PC. A binomial test was used to examine the difference between the observed number of affiliative behaviors and the number expected by chance. We compared the number of times that each role (e.g., the aggressor, the recipient of aggression, the bystander) was the actor in contact swimming using the Wilcoxon signed-rank test ('exactRankTests' package; Hothorn & Hornik, 2019). All statistical analyses were conducted using *R*, Version 4.1.2 (The R Foundation for Statistical Computing).

Results

Aggressive events were observed approximately 0.83 times per hour (a total of 616 aggressive events), and we collected data from 109 PC periods. Among the three affiliative behaviors, parallel swimming was observed most frequently (parallel swimming, 104 PCs; contact swimming, 39 PCs; flipper rubbing, 23 PCs). The occurrence rate differed among parallel swimming, contact swimming, and flipper rubbing (Fisher's exact test, $p < 0.001$). Parallel swimming occurred more frequently than expected (binomial test, $p < 0.001$), while contact swimming and flipper rubbing occurred less frequently than expected (binomial test: contact swimming, $p = 0.004$; flipper rubbing, $p < 0.001$).

Parallel swimming was observed most often within 1 min after the end of aggression (70% of 104 times), and it decreased more than 1 min after aggression (Figure 1). Contact swimming was observed most often within 1 min after the end of aggression (54% of 39 times), and it decreased more than 1 min after the aggression (Figure 1). Flipper rubbing was infrequently observed within 1 min after the end of aggression (4% of 23 times), and it was observed most often 1 to 2 min after the end of aggression (43% of 23 times; Figure 1).

In contact swimming between former opponents, the recipient of aggression was the actor in 77 ± 42% of cases ($n = 9$ times; average ± SD). The assumed role of the actor did not differ between the aggressor and the recipient of aggression (Wilcoxon signed-rank test, $n = 6$ pairs, $V = 2.5$, $p = 0.31$). In contact swimming between the aggressor and the bystander, the aggressor was the actor in 22 ± 29% of cases ($n = 9$ times). The assumed role of the actor did not differ between the aggressor and the bystander ($n = 4$ pairs, $V = 0$, $p = 0.5$). In contact swimming between the recipient of aggression and the bystander, the recipient of aggression was the actor in 67 ± 41% of cases ($n = 24$ times). The assumed role of the actor did not differ between the recipient of aggression and the bystander ($n = 10$ pairs, $V = 13.5$, $p = 0.20$).

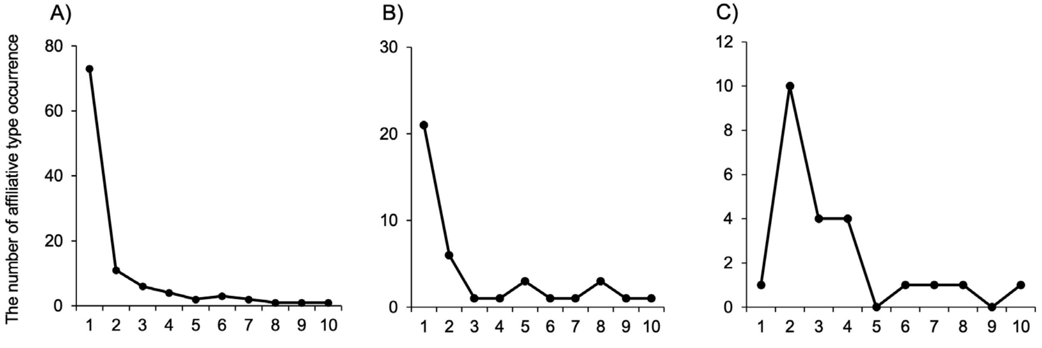

Figure 1. Temporal distribution of (A) parallel swimming, (B) contact swimming, and (C) flipper rubbing observed in captive bottlenose dolphins (*Tursiops truncatus*), including five adult females and three calves, from the Kagoshima City Aquarium, Japan

Discussion

The occurrence frequency after aggression differed among parallel swimming, contact swimming, and flipper rubbing. Parallel swimming was commonly seen after aggression, and this behavior occurred more frequently than expected. It was likely to occur within 1 min after aggression. This result indicates that parallel swimming often occurred immediately after aggression. Contact swimming occurred less frequently than expected, but it was likely to occur 1 min after aggression. This result indicates that contact swimming occurred immediately after aggression, but its frequency was lower than parallel swimming. A previous study suggested that affiliation with former opponents that occurred immediately after aggression functioned as a tension reduction strategy (Yamamoto et al., 2015). Bottlenose dolphins may engage in parallel swimming and contact swimming when they try to reduce the tension of aggression.

Although contact swimming occurred immediately after aggression, contact swimming occurred less frequently than parallel swimming. This might be due to the difficulty in touching while swimming. Swimming with touching requires precise coordination of the movements between two individuals. Another plausible reason is that cohesion is easier than touch. When social tension is high after aggression, former opponents allow cohesion for parallel swimming but may not allow touch with their bodies.

Although flipper rubbing minimized renewed aggression (Tamaki et al., 2006), common bottlenose dolphins may rarely engage in flipper rubbing within 10 min after aggression. After tension reduction, dolphins may engage in flipper rubbing for social bonding (Dudzinski & Ribic, 2017). Although three affiliative behaviors occurred after aggression, the frequency or latency of occurrence differs among these behaviors. The function may differ among these affiliative behaviors, and dolphins may engage in a specific behavior after aggression. To test whether conflict intensity affects affiliative behaviors, and whether the latency of the next conflict differs among affiliative behaviors, the function of each affiliative behavior will be shown in more detail.

In some primates, the recipient of aggression tends to feel more stress than the aggressor (Aureli, 1997), and bystanders might be responsive to the stress of the recipient of aggression (Fraser et al., 2008). The tension that dolphins feel after aggression may also differ among the aggressor, the recipient of aggression, and the bystander. Contact swimming may occur when individuals feel stressed (Connor et al., 2006). Although it is unclear whether both actor and receiver reduce the stress by contact swimming (Connor et al., 2006), the status of the individuals may affect the role of contact swimming. The frequency of the recipient of aggression being the actor tended to be higher than the frequency of the bystander being the actor. However, the number of times that the individual was the actor did not differ significantly between the aggressor and the recipient of aggression, between the aggressor and the bystander, or between the recipient of aggression and the bystander. The sample size of contact swimming was small. Further studies are needed to investigate whether the tension for individuals affects the actors of contact swimming with the goal to examine the function of affiliation in detail.

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