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RESEARCH REPORT

Intra- and inter-group aggression of wild bonobos

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要旨

ヒトの攻撃性の進化を語る上で、遺伝的に近縁であるチンパンジー（*Pan troglodytes*）がしばしば比較対象とされてきた。チンパンジーのオス間では、発情メスを巡ってや社会的地位の上昇などのために、非常に激しい闘争が観察される。彼らは連合（"coalition"）を組み、策略を巡らせて、順位が上の個体を失脚させることが知られている。メスは全てのオスより順位が低い。群れ間は激しい敵対関係にあり、縄張りの境界では激しい闘争が起こる。オスたちは結託し、他の群れの個体を殺すこともある。しかしながら、ヒトにはもう一種、進化の隣人がいる。ボノボ（*Pan Paniscus*）はチンパンジーと非常に近縁でありながら、社会行動は大きく異なっている。攻撃交渉は穏やかであり、オスたちが連合を組んで争うことはほとんどない。一方、メス達が連合を組んでオスと対抗することで、メスの社会的地位は高い。他の群れと出会っても、激しい闘争は見られない。ヒトの攻撃性の進化を理解する上で、ボノボの攻撃性の理解は重要だが、研究は進んでいない。コンゴ民主共和国赤道州にあるルオー科学保護区の野生ボノボを対象に、攻撃交渉のパターンや激しさを明らかにし、群内、群間の攻撃交渉を比較することを目的として研究を行った。

野生ボノボの集団 Pe グループとその隣接群を対象に 588 時間の観察を行った。観察中、全ての攻撃交渉を記録した。2 頭以上が一緒に同じ個体を攻撃したとき、"連合攻撃 (Coalitionary aggression)"として記録した。

284 回の群れ内攻撃交渉と、51 回の群れ間攻撃交渉を観察した。群れ内攻撃交渉では、オス間の攻撃交渉が非常に多く観察された。攻撃交渉への参加率のみ見るとメスの攻撃性はオスに比べて低いが、メスが攻撃に参加した場合、身体接触を伴う激しい攻撃になる割合が多かった。連合攻撃行動は、メス間に多くみられ、全てオスを攻撃するために組まれたものだった。第一位のオスがメス達の連合に激しく攻撃され、大幅に順位を下げる様子を観察した。

群れ間の攻撃では、身体接触を伴う攻撃の割合は群れ内攻撃よりも低かったにも関わらず、個体が怪我をする割合は群れ内の攻撃より高かった。群れ間攻撃交渉では、群れ内攻撃交渉に比べ、メスが攻撃に参加する割合が大きかった。連合攻撃を行う割合は、群れ内攻撃交渉より、群れ間攻撃交渉の方が多かった。面白いことに、違う群れのメス同士が連合を組んで、オスを攻撃する行動が見られた。

ボノボの群れ間攻撃交渉は、チンパンジーのそれと比べると、非常に穏やかなものであった。個体を死に至らしめるような攻撃は一度も観察されなかった。怪我の割合や連合攻撃の多さから、ボノボは他の群れの個体の存在に対して必ずしも寛容である訳ではないということが分かった。しかしながら、メスにとっては、群れの一員として振る舞うよりも、「オス」を共通の「敵」としてメス同士で協力しあうことの方が重要なのかもしれない。メスは攻撃交渉への参加率は低いが、連合を組み、オスに激しい攻撃を加えることで、オスの攻撃性を抑制していた。メスの攻撃性が、ボノボの群内、群間攻撃交渉を理解する上での鍵となるだろうことが示唆された。

メインのテーマ以外に、調査地では初めて、野生ボノボ全体でも二例目となるカニバリズム（同種食い）を観察したので報告する。

Abstract

Aggressiveness and warfare of humans are often compared with one of our closest relatives, the chimpanzees (Pan troglodytes). Chimpanzee males fight severely to attain higher social rank, and acquire or protect limited resources like food or sexual partner. They often make coalition to attack the competitors and sometimes beat them to death. All males possess the higher social status than that of females, and infanticides by males are observed. The inter-group relationship is quite oppositional, and they sometimes kill the members of other group. However, in our other closest relative, bonobos, the aggressive interactions are much milder than in chimpanzees. Severe aggressive interactions like those in chimpanzees do not occur even during the inter-group encounters. When they encounter with other group, they can peacefully stay together for several days. Despite the importance of understanding the aggressive interactions, studies of aggressive interactions in bonobo are scarce. I studied the intensity of aggressive interactions and pattern of coalition in wild bonobos and compared the difference between intra- and inter-group aggressions.

I studied a group of bonobos (Pe group) and bonobos of neighboring group at Luo Scientific Reserve, DR Congo. I followed a party of bonobos for 588 hours and recorded all aggressive interactions. If two or more individuals jointly attacked the same target(s), I recorded the attack as coalitionary aggression.

284 intra-group aggressive interactions were recorded. Non-serious injury was observed twice. Male-male aggressions were most frequently observed pattern of aggressive interaction. Females attended the aggressions much less than males. However, when females took part in the aggression, it tended to be physical. All coalition were formed to attack male(s). Female-female pair formed coalition much more than male-male and male-female pairs. Impressively, I observed the downfall of alpha-male and it was caused by four female's severe aggression toward him.

Pe group encountered with Pw group 17 times and with Gr groups 7 times. 51 inter-group aggression were recorded. Though the proportion of the physical aggression was much lower in inter-group aggressions, individuals of Pe group got injured during the encountering three times. The frequency of forming coalition was higher in inter-group aggression that that in intra-group aggressions. Same

as intra-group aggressions, all coalition were formed to attack male(s). The frequency of injury was much higher in inter-group aggression than that in intra-group aggression. Interestingly, females from deferent groups formed coalition to attack male(s).

Inter-group aggressions of bonobos were much milder than those of chimpanzees. Serious aggressions which were possibly lethal were never been observed. The possibility of injury and the probability of forming coalition suggested that bonobos are not completely tolerant toward individuals of other groups. However, for females, "males" might be "common enemy", and the female coalition might be more important than membership of group. By forming coalition, females could beat males and control males' aggressiveness. Female's aggressiveness might be the key to understand both intra- and inter-group aggressions in bonobos.

In addition to the main theme, I report the filial cannibalism in bonobos. This is the first case in my research site and second case in wild bonobos.

Introduction

Aggressiveness and warfare of humans are often compared with one of our closest relatives, the chimpanzees (*Pan troglodytes*), because the two species show considerable similarities in these issues. Chimpanzee males fight severely to attain higher social rank, and acquire or protect limited resources like food or sexual partner. They often make coalition to attack the competitors and sometimes beat them to death (Wilson et al. 2014). All males possess the higher social status than that of females, and infanticides by males are observed. Also, the inter-group relationship is quite oppositional in chimpanzees. They show severe aggressive interactions when they encounter, and it is reported that males form coalition to attack, or sometimes kill the members of other group (Wilson et al. 2014).

However, we have to consider the behaviors of our other closest relative, the bonobos (*Pan paniscus*), to understand aggressiveness in humans. In bonobos, the aggressive interactions are much milder than in chimpanzees. It is known that bonobo males seldom form coalition for aggression (Furuichi 1997, Ihobe 1992). On the other hand, coalition between females is often observed and considered to be important to maintain their high social status (Parish1996, Furuichi 2011, White and Wood 2007). Infanticide in bonobos have been never observed. Severe aggressive interactions like those in chimpanzees do not occur during the inter-group encounters. When two or more groups encounter, first they get excited and threat or chase each other. However, after a while they become calm and stay together peacefully. They feed, groom or play together (Idani 1990). Even males from different groups sometimes groom or play each other.

Despite the importance of understanding the aggressive interactions, studies of aggressive interactions in bonobo are scarce, probably because of the low occurrence rate of aggressive interactions. The aim of this study is to clarify the intensity of aggressive interactions and pattern of coalition in wild bonobos, and compare intra- and inter-group aggression.

<Figure 1 Chimpanzee males>

<Figure 2 Bonobo females>

Study Area

The study area was Wamba, Luo Scientific Reserve, Democratic Republic of the Congo (0° 11′ 08″ N, 22° 37′ 58″ E). At Wamba, northern area of Luo Scientific Reserve, research of bonobos have been conducted since 1973. Approximately 3000 people are living in Wamba village. Villagers have a strong taboo of eating bonobos, so bonobos were well reserved even before the scientific reserve established. Villagers are allowed to conduct traditional use of forest, but use of gun or metallic trap

were restricted. Japanese researchers are conducting local contribution activities. For example, we established the local hospital and scholarship system.

< Figure.3 Research Camp>

Methodology

Study subjects

My main study subjects were wild bonobos of Pe group. Pe group consists of 25 individuals including 9 adult females and 6 adult males. All of the individuals are identified and fully habituated. I also observed bonobos of E1 group, Pw group and Bi group when Pe group encountered with them. Bonobos of E1 group and Pw group were identified and fully habituated. E1 group consists of 36 individuals including 10 adult males and 10 adult females. Pw group consist of 14 individuals including 5 adult males and 4 adult females. Bonobos of Bi group were not fully identified nor habituated. At least 20 individuals were in the group.

Observation Method

I followed a party of bonobos and recorded all aggressive with helps of two local assistants. When the party split, I tried to follow the largest party. An interaction including at least one aggressive behavior was defined as aggressive interaction. Aggressive behaviors are as follows: vocal or non-vocal threating, charging, chasing and physical attack (Kick, beat, grabbing etc.). Submissive behavior is as follows: avoiding, jump aside, fleeing, screaming and grimacing. If two or more individuals jointly attacked one or more recipient(s), I recorded the attack as coalition. When the individual(s) of another group was observed during the observation of Pe group, I defined that Pe group encounter with another group. During the group encountering, I recorded all aggressive and affiliative interactions.

I used notebooks and a pen for recording. When I observed rare events, I used a video camera.

Research findings

Intra- and inter- group aggression of wild bonobos

I observed parties of bonobos for 588 hours. 284 intra-group and 51 inter-group aggressive interactions were recorded. Pe group encountered with Pw group 17 times and with Bi groups 7 times. They never encountered with E1 group.

Intra-group aggressions

239 aggressive interactions were occurred between adult individuals. 162 aggressive interactions were male-male aggressions, 8 were female-female, 69 were inter-sex aggressions. Of 69 inter-sex aggressions, females won against males in 33 aggressions and males won against males in 12 aggressions. In 24 aggressions, the recipients of the aggression did not show submissive behaviors.

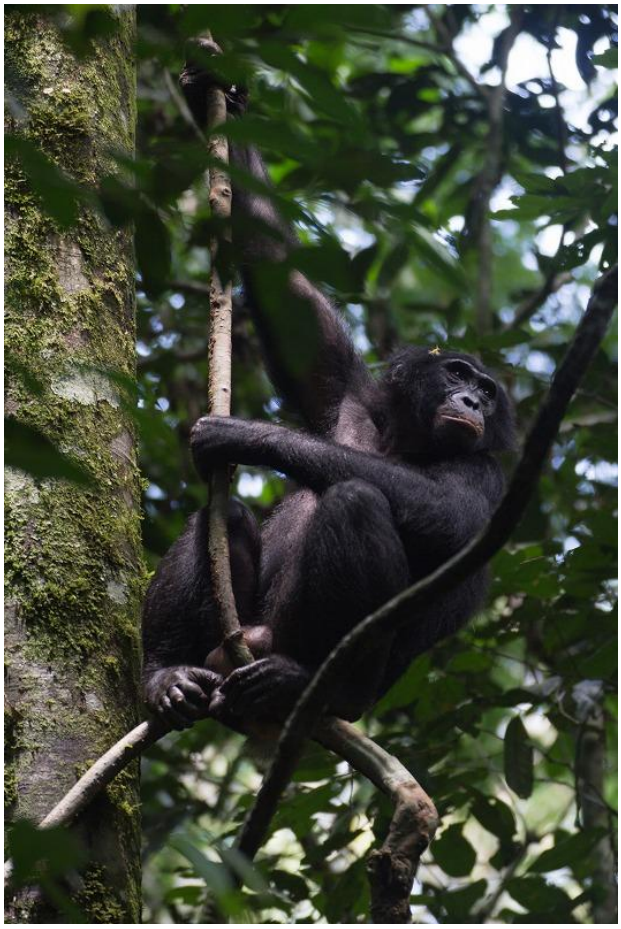
48 physical aggression were observed (26 male-male, 3 female-female and 19 intersex aggressions). The proportion of physical aggression was higher when female(s) took part in the aggression (overall: 20%, male-male: 16%, female-female: 37%, intersex: 27.5%). Males never attacked females physically. Most of physical attacks were not serious. Injury was observed twice:

Case 1: An old female "Bokuta" attacked a juvenile female, and her mother charged the female to help her daughter. However, Bokuta counterattacked and bit the mother. She bled from her left hand, but the injury was small.

Case 2: An alpha-male (highest rank male) "Snare" was displaying around an estrus female. The estrus female and 2 other females charged and chased around the male for 4 minutes. Snare tried to flee, but females caught him. One female bit his hand, other two females bit his leg. Females kept biting him for more than 30 seconds but finally he fled and run away. Because of this aggression, he lost his forefinger of right foot.

27 coalitions were observed. 3 coalitions were formed by males, 12 by females and 12 by both sexes. All of the target(s) of coalition was male(s). Bonobos never formed coalition to attack female nor juvenile.

As I mentioned above (case 2), the alpha-male Snare was attacked by 3 females and lost his toe. He was not observed for 19 days. When he came back to the group, he was not highest rank male anymore. He showed submissive behavior to other males. His rank dropped to at least 3rd ranking for sure, possibly 4th ranking.



<Figure 4: Snare>

Inter-group aggressions

49 aggressive interactions were observed between Pe and Pw group. 2 aggressions were observed between Pe and Bi group. 19 male-male, 2 female-female, 31 intersex aggressions were observed. In 44 aggressive interactions, the individual(s) of Pe group won against the individual(s) of Pw group. In both 2 aggressions, Pe individuals won against Bi individuals.

Only three physical aggressions were observed. The proportion of the physical aggression was much lower in inter-group aggressions (intra-group aggression: 20%, inter-group aggression: 5.9%). I could not observe directly, but I observed individuals of Pe group got injured during the encountering three times.

Case 1: An old female "Bokuta" was observed to be injured her right arm seriously during the encounter with Pw group. Her wound was approximate 6cm long and 3cm width.

<Figure 5: Bokuta's injury>

Case 2: A low rank male was observed to be injured his right toe during the encounter with Bi group. He lost his right toe.

Case 3: An old female was observed to be injured her left arm. Her wound was approximate 3cm long.

12 coalitions were observed. The proportion of forming coalition was higher in inter-group aggressions than intra-group aggressions (intra-group: 11.3%, inter-group: 24.5%). Same as intra-group aggressions, all coalitions were formed to attack males.

Females of Pe and Pw group formed coalition together to attack males 3 times.

Discussion

Intra-group aggressions

I found that male-male aggressions were most frequently observed. Females attended the aggressions much less than males. Aggressiveness of females seems much lower than that of males if only the rate of attendance to the aggressions were considered. However, when females took part in the aggression, it tended to be physical. The causes of two injuries which I observed during the intra-group aggression were both female's aggression.

All coalitions were formed to attack males. In chimpanzees, males often form coalition to acquire higher rank, but in bonobos, females formed coalition more actively than males did (corresponding to the result of previous study: Furuichi 1997, Stevens 2006).

The occurrence of downfall of the alpha-male "Snare" was quite impressive. He had been keeping his alpha-position at least since 2012, when I started observation. The reason of his downfall was severe

aggression by female coalition. In chimpanzees (primates generally), males compete to acquire higher rank and estrus females (e.g. Cowlishaw & Dunber 1991). They sometimes form coalition to bring down the competitors (e.g. Wilson et al. 2014). In long-term study site of chimpanzee, Mahale, there was a case that males formed coalition and killed the alpha-male (Kaburu & Inoue 2013). However, in chimpanzees, females do not take part in the males' competition.

In bonobos, Furuichi (1997) claims that mothers help their sons to acquire higher rank. It is possible that mothers attacked Snare to improve their son's rank. However, ongoing DNA analyzing revealed that all three females who attacked Snare was not the mother of new alpha-male. Females might attacked him merely because he behaved aggressively around females, and annoyed them. One hypothesis claimed that coalitions among females to protect an adult female against an attack by a male may be useful for females since it warns males that hostility to females is risky (Hemelrijk & Steinhauser 2007). My observation clearly supported this hypothesis.

Comparison of intra- and inter-group aggressions

In chimpanzees, most aggressors and recipients of inter-group aggressions are males (Wilson et al. 2014). However, I found female's high attendance to inter-group aggressions. The proportion of inter-group physical aggressions was much lower than that of intra-group aggressions. However, 3 injuries were observed and these were more serious than the injuries by intra-group aggressions. Attacking physically to unfamiliar individuals might possibly end up serious injuries, so bonobos might refrain to attack physically. The injuries were not small, though much milder than those of chimpanzees' injuries. No injuries that might cause death of recipients were observed.

Proportion of coalition formation was higher in inter-group aggressions than that in intra-group aggressions. This might suggest that they had motivation to protect their resources (ranging area, food etc.). They were not completely tolerate to the presence of another group. However, interestingly, females of different group formed coalition to attack males. It might means that for females, the membership of the group was not so important. For them, males were the "common enemy" and they can cooperate beyond the group.

It seems that female aggressiveness is the key to understand their intra- and inter-group aggressions. Males took part in the aggressive interactions much more than females, but they just chase or display each other. Behaving aggressive is risky to males because females can form coalition to attack aggressive male. This female aggressiveness toward males may be one reason that male's aggressiveness was constrained in bonobos.

Bonobos can be peaceful with another group (Idani 1990), but they were not completely tolerate to the another group's individuals. The injuries of inter-group aggression were more serious than that of intra-group aggression. Risk of engaging inter-group aggression was smaller in bonobos than that in chimpanzees, but still risky enough to avoid physical aggression. Females can form coalition with another group's females to attack males. This might means that for females, membership of the group is not so important.

Since aggressive interaction in bonobos occurs not frequently and inter-group encountering is rare, more effort and long-term observation are needed to understand the difference between intra- and inter-group aggressions.

Another Research finding

Filial cannibalism in wild bonobos

Introduction

On 11th March, I observed filial cannibalism in wild bonobos. Though it was not related to my main theme, this observation was very important to understand the nature and mind of bonobos, and worth reporting.

Cannibalism have been observed in various animal taxa, but very rare in primates. In primates, most cases were observed in Chimpanzees that males ate infants after infanticides. However in chimpanzees, filial cannibalism, which is the behavior that a mother eats her own infant, were never reported. Filial cannibalism in primates had been only observed under stressful condition, such as laboratory galagoes (Tartabini 1991), rehabilitated Orangutans (Dellatore et al. 2009). In bonobos, cannibalism had not been observed for a long period. However in 2008, cannibalism in wild bonobos was observed at Lui Kotale, Salonga national park, DR Congo. One year old dead infant was eaten by her mother and other individuals. The mother was a low rank female, and the carcass was taken from her by higher rank individuals (Fowler & Hohmann, 2010). It was the first cannibalism report in bonobos and also in wild primates. My observation was second filial cannibalism in wild bonobos, and also in wild primates.

Description

A mother *Hide*, who was an old and high rank female gave birth between 9th and 10th March. I could not confirm the reason of death, but when I first observed the infant at 8:40 of 11th March, the infant was already dead. It already started decomposing, and corrupt smell was in the air. No injury to the body of both infant and mother was observed.

8:40-14:03

Hide was holding the dead infant. She traveled together with other individuals, fed, took rest as ordinary days. When two unrelated infants came to see and touch infant, *Hide* flipped them using her hand.

14:04

Hide was traveling on the ground. Other bonobos climbed up to feed fruit, but *Hide* sat on the ground. She suddenly put the dead infant in her mouth, bit of its head with one bite. Her older juvnile son, *Hideo*, peered touched *Hide*'s mouth to beg. *Hide* put a piece of meat from her mouth and gave *Hideo*.

<Figure 6: Hide and Hideo eating dead infant>

14:09

An adult female, *Ichi*, approached Hide. Hide did not give meat to her. She took a piece of meat from *Hideo*. *Hideo* showed submissive facial expression to her.

14:24

Hide stopped eating the carcass. She ate the infant's head and body. *Hideo* took the limbs and started eating.

14:38

Hideo finished eating all of meat which he got. Bonobos started traveling on the ground.

Discussion

Filial cannibalism in primates have been considered to be aberrant behavior since the behavior had been observed only under the stressful conditions such as laboratory or provisioned. However, the first filial cannibalism in wild primates was observed in bonobos at Lui Kotale (Flower & Hohmann 2010), and second case was also observed in bonobos (this case) at Wamba. Two filial cannibalism were observed in wild bonobos of different two field sight within less than 10 years might mean that filial cannibalism is not aberrant behavior in bonobos.

In chimpanzees, cannibalisms were observed usually after infanticides. Infants were taken by another individuals (mostly males), killed and eaten. However, there is no report of filial cannibalism in chimpanzees. There are several reports that mothers of chimpanzees carried the dead infant for long period, and took care of them as they were alive (Biro 2011). In bonobos, they often carry the dead infant for 2-3 days, but long carriages like chimpanzees have never been observed.

It was interesting that the reaction of the mother to the dead infant was opposite between these two close related animals. Does a bonobo mother consider her dead infant as a food (or a meaningless object), and chimpanzee mother moan her infant's death? Do they understand the concept of death? This observation shed a new light on understanding the cognitive ability of bonobos and chimpanzees.

Reflection on the GLTP in Africa

I had a seminar at University of Kinshasa on 14th January. The primatology section was established three years ago, and now they have several master course students. I and Prof. Mbomba discussed about the future studies that the students could conduct. About 50 students of biology department came to attend our seminar. I presented about bonobo's aggressive behaviors. It might be a little bit difficult for students because most of them were under-graduated and their official language was French. However, they listened with keen interest and gave me questions actively. I heard that some students are now interested in studying the social behaviors of bonobos. Before and after the seminar, I had meetings with professor Mbomba, Professor Malekani (head of the biology section), Dr. Mbangi (the senior researcher of Research Center of Ecology and Forestry, studying ecology of bonobos) and master course students.

Also, I had another meeting with professor Mbomba on 2nd July when I came back from the field. It was really good opportunity for me that I could discuss with professors of University of Kinshasa. Our research team and University of Kinshasa have been engaging the partnership, but I myself had never discussed about the collaboration research with them. With help of GLTP program, I could present my research idea to professors and discussed the possibility of collaboration study with them. For example, Prof. Mbomba proposed the idea that analyzing the chemical components of bonobo foods and exploring the possibility of self-medication in bonobos. This theme is a little different from my research interest, but it is possible that I take the sample in the field and students in University of Kinshasa analyze the chemical components.

We promised to keep in touch, and discuss more about our future collaborations. I'd like to contribute the development of primatology and animal ethology in DR Congo.

<Figure 7: Lecture at University of Kinshasa>

Acknowledgment

I would like to thank professors in UN University: Dr. Saito, Dr. Imai and Dr. Nakano, for giving me great opportunity to study in Africa. I thank Dr. Mbomba and Dr. Furuichi for their supervising. I thank Dr. Sakamaki, Mr. Ryu, Ms. Graham, Mr. Toda and Ms. Yokotsuka for supporting me at Wamba. I thank local assistances and all the villagers in Wamba.

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