

# Harassment of adults by immatures in bonobos (*Pan paniscus*): testing the Exploratory Aggression and Rank Improvement hypotheses

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**Abstract** The immatures of many primate species frequently pester adult group members with aggressive behaviors referred to as a type of harassment. Although these behaviors are characteristic of immatures as they develop from infancy through adolescence, there have been few studies that specifically address the adaptive significance of harassment. Two functional hypotheses have been generated from observations of the behavior in chimpanzees. The Exploratory Aggression hypothesis describes harassment as a mechanism used by immatures to learn about the parameters of aggression and dominance behavior and to acquire information about novel, complex, or unpredictable relationships. The Rank Improvement hypothesis describes harassment as a mechanism of dominance acquisition used by immatures to outrank adults. This study investigated harassment of adults by immatures in a group of bonobos housed at the Columbus Zoo and compared the results to the predictions outlined by the Exploratory Aggression and Rank Improvement hypotheses. Although all immature bonobos in this group harassed adults, adolescents performed the behavior more frequently than did infants or juveniles and low-ranking adults were targeted more frequently than high-ranking. Targets responded more with agonistic behaviors than with neutral behaviors and the amount of harassment an individual received was significantly correlated with the amount of agonistic responses given. Furthermore, bouts of harassment were found to continue significantly more frequently when responses were agonistic than when they were

neutral. Adolescents elicited mostly agonistic responses from targets whereas infants and juveniles received mostly neutral responses. These results support predictions from each hypothesis where harassment functions both as a mechanism of social exploration and as a tool to establish dominance rank.

**Keywords** Infant and juvenile behavior · Development of aggression · Agonistic behavior

## Introduction

The infants, juveniles, and adolescents of many species of non-human primates are known to exhibit a type of behavior, where they routinely pester adult group members, often provoking an aggressive response (e.g., baboons: Rowell 1967; langurs: Dolhinow 1972; Java monkeys: de Waal 1977; vervets: Bramblett 1978; and chimpanzees: de Waal and Hoekstra 1980; Pusey 1990; Nishida et al. 1999). Observations of such behavior by immatures range from mild aggression, such as throwing sand, dirt, and branches at adults (de Waal and Hoekstra 1980) to more aggressive contact, such as jumping onto resting adults and biting, kicking, and pulling their hair (van Lawick-Goodall 1968) and/or tails (Bramblett 1978). Although referred to in the literature with a variety of terms, including ‘bothering’, ‘teasing’, ‘annoying’, ‘provocative’, ‘quasi-aggression’, and most recently as ‘harassment’, the central feature of these behaviors is the potentially harmful or unpleasant stimuli it provides to the recipient (Adang 1984).

The first accounts of what could be described as harassment of adults by immatures in chimpanzees came from Hebb and Thompson’s (1954) early descriptions of

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“anger” in a captive group and from van Lawick-Goodall’s (1968) studies of the wild chimpanzees of Gombe, where young juveniles in both studies were observed aggressively pestering resting and grooming adults. De Waal and Hoekstra (1980) remarked in their study of the contexts of aggression in chimpanzees, that juveniles and infants would regularly tease adults, who would often respond with aggression. Although such mention of harassment behaviors were somewhat common, it was not until Adang’s (1984, 1985) studies of the Arnhem group of chimpanzees that the ethology and contextual parameters were formally described. Initially calling the behavior ‘quasi-aggression’, because it had “elements in common with both play and aggression”, Adang (1984, 1985) defined harassment by immatures as any type of aggressive bothering behavior directed at adults irrespective of the response generated. Adang (1985) noted that “individuals responded in many ways, including occasional punishment in the form of retaliation”. He further differentiated harassment from other forms of immature aggression by identifying the context as “spontaneous and ... that [which] does not occur in close temporal association with conflict between any individuals in the group” (Adang 1984). Harassment by immatures, therefore, poses an interesting evolutionary question because of the inherent risks associated with retaliation, particularly when an adult target directs aggression toward smaller immature individuals.

Addressing this question of adaptive significance, Adang (1984, 1985) explored the mechanistic properties of harassment by investigating the type of behavior performed by immatures and the response behavior of targets at Arnhem. He found that all immatures harassed adults and directed their behaviors mostly at individuals outside of their immediate subgroup, consisting of their mother and closely associated female(s) that provided a degree of allo-maternal care (Adang 1984). Although all adults in the group were targets, he observed that males were more likely to receive mild aggression such as ‘bluff-like’ behaviors while females more frequently received behaviors with physical contact, such as hitting and kicking. Adang (1984) also found that certain responses to harassment were reinforcing in nature where the amount of harassment a target received was dependent on the type of response given. He observed that harassment would continue for longer if the target responded in an agonistic way (either aggressively or submissively) whereas friendly behaviors and ignoring the immature generally resulted in the cessation of harassment. From these results, Adang (1984, 1985) hypothesized that harassment is a form of social exploration used by immatures to learn about and refine aggressive behaviors, and to acquire information about the relationship between the actor and lesser-known individuals.

Currently referred to as the Exploratory Aggression hypothesis, Adang (1985) proposed two functional forms of exploratory aggression: (1) investigating authority and (2) reducing uncertainty. Investigating authority functions mainly as a way for immatures to acquire knowledge about the parameters of dominance by directing mild forms of harassment behavior at high-ranking group members (i.e., male chimpanzees) and to explore the properties of physical contact aggression by directing these types of harassment behaviors at lower-ranking group members (i.e., female chimpanzees) (Adang 1985). The second functional form, reducing uncertainty, is expressed in a manner similar to the way in which immatures learn about and explore the physical world (Adang 1985). In reference to the observation by Seligman (1975) that animals attempt to control their environment and to predict events before they happen, Adang (1985) hypothesized that immatures use harassment to reduce existing uncertainty in relationships by either controlling or predicting the response of targets. Both submissive and aggressive reactions provide information about dominance relationships that immatures can use to predict the behavior of targets. Eliciting submission may also reflect an immature’s ability to control the response of the target (Adang 1985). Ignoring or making friendly contact with an immature, however, does not provide information about dominance relationships and is, therefore, not implicitly reinforcing in the context of harassment (Adang 1985). The Exploratory Aggression Hypothesis (1984, 1985) was initially formulated to describe harassment of adults as a mechanism through which infants and juveniles reduced relationship uncertainty, although Adang (1986) noted that as individuals matured, these behaviors might be used as a means for adolescents to exercise control (i.e., elicit submission) over adults as they begin to establish dominance.

Harassment of adults by immatures has also been documented in wild chimpanzees at the Gombe (Pusey 1990) and Mahale (Nishida et al. 1999) field sites. Contextualized as a threatening behavior, researchers at both sites recorded juvenile males spontaneously aggressing adult females, mainly through display-type behaviors such as waving branches and throwing stones, and noted that these behaviors increased in frequency as the males matured into adolescence (Pusey 1990; Nishida et al. 1999). It was not until a later study at Mahale, however, that the behavior was specifically addressed between immature males and adult females (Nishida 2003). Referred to as the Rank Improvement hypothesis by Nishida (2003), responses in this study were classed as either ‘ignore’ or ‘not ignore’, and as either ‘retaliate’ (which included both aggressive and submissive behaviors) or ‘not retaliate’. Nishida (2003) reported that duration of harassment was longer when targets reacted to harassment than when they did not react.

Although adult female targets frequently ignored juvenile males, they mostly responded with defensive and avoidance behaviors when harassed by adolescent males (Nishida 2003). In addition, immature males harassed more frequently than did females and targeted adult females significantly more than adult males (Nishida 2003). Evidence of adolescent male chimpanzees dominating females as a precursor to entering the male dominance hierarchy is well known (Goodall 1986; Nishida 1990) and harassment at Mahale was, therefore, interpreted as a mechanism of rank improvement used primarily by immature males as a means to outrank adult females (Nishida 2003).

Harassment of adults by immatures, to our knowledge, has only been investigated in detail in chimpanzees (captivity: Adang 1984, 1985; wild: Nishida 2003). Despite small differences in definitions and composition of study groups, there are general consistencies between the Arnhem and Mahale studies in the pattern of responses to harassment that can shed light on how harassment functions within a particular social system. Results from both sites showed that immatures frequently harass adult group members and that continuation of harassment was dependent on the type of response given by the target (Adang 1984, 1985; Nishida 2003). Additionally, females from both sites were targeted more than males and responded more frequently with agonism whereas males responded more with neutral behaviors (Adang 1985; Nishida 2003). These results suggest that harassment in chimpanzees is influenced by the sex-based dominance structure of the species, where the lower ranking sex (females) is targeted more frequently and responds in a manner consistent with harassment as a challenge to their dominance status. In order to examine the degree to which this pattern is dependent on social system and to test the assumptions of the Exploratory Aggression and Rank Improvement hypotheses, detailed observations of harassment in species with markedly different social structures are needed.

The purpose of this study, therefore, is to describe the pattern of harassment of adults by immatures in bonobos and to discuss the proposed functions of the two competing hypotheses within the context of the bonobos' unique social system. Instances of adolescent males provoking adult males with harassment behaviors have been observed in the wild population at Wamba (Furuichi 1997). Furuichi (1997) described these exchanges as 'play-like agonistic interactions' (p. 862) and considered them to be similar to the quasi-aggressive behaviors of chimpanzees reported by Adang (1985). Harassment of adults by immatures, however, has not yet been studied in detail in this species. Bonobos, like chimpanzees, are male philopatric and exhibit a multi-male multi-female fission–fusion community structure (Nishida 1968; White 1988; Kano 1992). There are, however, distinct differences between the two

species, particularly in the types of social bonds displayed and complexity within the dominance hierarchy. Female bonobos, unlike female chimpanzees, form strong bonds with both males and females (White 1998; Hohmann et al. 1999) and can occupy the highest rank positions (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016). In chimpanzee communities, sex plays a defining role in the group dominance hierarchy where each male out-ranks each female (Goodall 1986; Nishida 1990). In bonobos, male rank can be heavily influenced by factors other than sex, which can result in variable dominance status (Kano 1992; Furuichi 1997; White and Wood 2007; Surbeck et al. 2011). We therefore expect that the patterning of harassment behavior in bonobos will reflect these similarities and differences to chimpanzees.

### Definition of terms

The following definitions are based on those originally given by Adang (1984, 1985) and reported by Nishida (2003) to describe harassment and response behaviors:

- **Immature harassment of adults:** from here on referred to as *harassment*, is any deliberate bothering or teasing type of aggression performed by immatures and directed at adults, irrespective of the response of the target individual and without any apparent cause or source of provocation. Although the term 'harassment' can be used to describe other types of aggressive behaviors in various contexts, such as 'sexual harassment' (e.g., Clutton-Brock and Parker 1995; van Schaik et al. 2004; bonobos: Hohmann and Fruth 2003), food 'sharing under pressure' (e.g., Stevens 2004), and harassment of immigrants (Pusey 1980; Watts 1992), the term 'harassment', for the purpose of this paper, will refer exclusively to the above definition. Following Adang's (1984) description, harassment type behaviors performed with a 'play-face' [or exhibiting any of the play behavior patterns described by Palagi (2006, see Table 3)], those performed as a direct response (within 2 min) of an aggressive initiative, or within 2 min of an agonistic event, and those directed towards individuals engaged in copulation or socio-sexual behavior were not scored as harassment.
  1. *Actor*—the 'harasser', an immature performing harassment behaviors directed at an adult
  2. *Target*—an adult receiving harassment behaviors from an immature
- Harassment behaviors were further categorized based on the qualitative features originally described by Adang (1984):

1. *Mild aggression*
  - (a) ‘bluff-like’: charging, dragging branches, swaying, stamping ground, etc.
  - (b) ‘swinging object’: manually wielding an object in the direction and proximity (within 2 m) of the target
  - (c) ‘throwing object’: tossing an object (grass, dirt, wood-wool, branches/leaves, etc.) at a target
2. *Physical contact aggression*: biting, hitting, kicking, pulling the hair, etc. of a target.

- **Responses to harassment:**

1. *Agonistic*—responses that indicate either a submissive or aggressive position by the responding target (Scott and Fredericson 1951; Hinde 1966).
  - (a) Aggressive: counter-attack type responses such as chase, charge, hit, bite, etc., performed with tense and brusque movements indicative of aggression
  - (b) Submissive: defensive type responses such as fleeing, screaming, gesturing, baring-teeth, presenting rump, etc., indicative of submission and performed without expressing any sign of aggression
2. *Neutral*—responses that do not overtly indicate a submissive or aggressive position by the responding target
  - (a) Ignore: no apparent reaction to harassment or a small response such as watching or facing away from harasser
  - (b) Avoid: leave the proximity of the harasser or to crouch, parry, or flinch without expressing aggression or submission
  - (c) Affiliative: friendly contact with the harasser such as playing, grooming, presenting for copulation or socio-sexual behavior such as genito-genital rubbing (‘gg rubbing’) without expressing signs of submission

## Hypotheses and predictions

As discussed above, there are two competing, but not mutually exclusive, hypotheses on the function of harassment behavior. Each generates a slightly different set of predictions.

## Hypotheses

- The *Exploratory Aggression* hypothesis describes harassment as a mechanism used by immatures to learn about the parameters of aggression and dominance behavior (i.e., investigate authority) and to acquire information about novel, complex, or unpredictable relationships (i.e., uncertainty reduction) (Adang 1984, 1985).
- The *Rank Improvement* hypothesis describes harassment as a mechanism of dominance acquisition used by immatures to outrank adults (Nishida 2003).

## Predictions

The *Exploratory Aggression* hypothesis (Adang 1984, 1985) predicts that:

1. All adults will be targets of harassment but immatures will less frequently direct harassment toward his/her own mother, and toward adult females that provide him/her allo-maternal care.
2. Type of harassment behavior performed by immatures will be dependent on the dominance rank of the target where lower ranking adults will more frequently receive physical contact aggression and higher-ranking adults will more frequently receive mild aggression.
3. Continuation of harassment will be dependent on type of response behavior, where both aggressive and submissive responses will elicit continuation of harassment more frequently than will neutral responses because aggressive and submissive responses present greater opportunity for immatures to learn how to control (i.e., elicit submission) and/or predict (i.e., elicit aggression) the behavior of targets, than do neutral responses.

The *Rank Improvement* hypothesis (Nishida 2003) predicts that:

1. Immatures will not harass adults they already outrank. Frequency of harassment, however, will be negatively correlated with the dominance rank of adults because immatures use harassment to ascend the dominance hierarchy.
2. Aggressive responses will elicit harassment more frequently from immatures than will submissive responses because submissive responses indicate submission from the target and aggressive responses indicate dominance or incomplete submission from the target. Neutral responses will not elicit harassment that differs from expected frequency values because neutral responses do not indicate dominance or submission from the target.

3. We further predict that type of response to harassment will be dependent on:
- dominance rank of the target where lower-ranking targets will respond more frequently with agonistic (aggressive and submissive) behaviors and higher-ranking targets will respond more frequently with neutral behaviors because lower-ranking targets are more likely to perceive harassment as a threat to their rank status; and
  - the age-class of the immature where older (i.e., adolescent) individuals will more frequently elicit agonistic (aggressive and submissive) responses and younger (i.e., juvenile and infant) individuals will more frequently elicit neutral responses because older immatures are more likely to represent a threat to the target's rank status.

Additional prediction:

- As discussed above, female bonobos can hold positions of power within the group (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016). Performance of harassment by immatures may, therefore, be biased toward immatures with high-ranking mothers, and we predict that frequency of harassment performed will be correlated with the dominance rank of adult females with offspring in the group.

## Methods

### Subjects and housing

All data were collected on the captive group of bonobos housed at the Columbus Zoo and Aquarium (CZA) in Columbus, Ohio, USA during 2011 (June 23–August 29) and 2012 (May 20–July 13). Daily observations usually began around 0730 hours and ended sometime between 1300 and 1700 hours resulting in 909 observation hours. At the time of the study, CZA had eight females and eight males that were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m<sup>2</sup> each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m<sup>2</sup> each), two off-exhibit outdoor enclosures (18.5 m<sup>2</sup> each) and a large naturalistic outdoor public viewing exhibit (57.9 m × 45.7 m, 2647.7 m<sup>2</sup>) with grass, mature trees, and an artificial stream and waterfall. The keepers at CZA managed the bonobos to simulate the species typical fission–fusion process of variable party composition. In the morning, bonobos were allowed access to each other and parties were set based mostly on individual bonobo association preferences. During this study

period most individuals, with the exception of two of the adult males (Jimmy and Donnie), had equal access to each other and all immatures had abundant opportunity to interact with all adults. This management process usually resulted in three parties that lasted for 2–3 days, and rarely changed on a daily basis or exceeded 4 days.

### Age classifications

Individual age classifications were assigned based on the descriptions of age-class characteristics of bonobos detailed by Thompson-Handler et al. (1984). For example, Thompson-Handler et al. (1984) described an infant as an individual that ‘keeps in frequent proximity to mother; commonly rides ventrally but also may ride dorsally during progression; nurses frequently’ (p. 349). Individuals were, therefore, categorized according to the following: 0–2 years = infant; 3–7 years = juvenile; 8–9 years = adolescent I; 10–12 years = adolescent II; and ≥ 13 years = adult. These age classes vary slightly from what was reported for a wild population (Kano 1992) and reflect the accelerated development that can occur in captivity where food resources are rich and abundant. Additionally, adolescents were split into two developmental categories: (1) adolescent I, where individuals begin to display the physiological characteristics associated with the transition of puberty such as ano-genital swelling in females and expansion in testicle size in males, but where both sexes are generally still non-fertile (Marson et al. 1991a, b; Stumpf 2011); and (2) adolescent II, where female ano-genital swellings are accompanied by menstruation and fertility, and where males undergo a significant growth spurt, including testicles that become larger, more pendulous, and are considered to be fully functioning. During the 2011 season there were two infants (one male, one female), three juveniles (one male, two female), two adolescent I's (one male, one female), and one adolescent II (male). During the 2012 season, two individuals changed age class where one juvenile female became an adolescent I and one adolescent I female became an adolescent II. For both the 2011 and 2012 seasons there were four adult males and four adult females (Table 1).

### Behavioral observations

Data were collected using focal follows and all occurrence sampling of agonistic and harassment events (Altmann 1974). A bout of harassment was considered terminated when the actor ceased performing harassment behaviors for 2 min. To examine the interaction between response type and likelihood of receiving further harassment, bouts were also scored as either ‘continued’, where the actor continued harassment after the initial response of the target, or

**Table 1** Group composition and age class assignments of the CZA bonobo colony (2011–2012)

Subject	Birth year	Sex	Adult rank	Age classes	
				2011	2012
Unga	1993	F	1	Adult	Adult
Ana Neema	1992	F	2	Adult	Adult
Donnie	1993	M	3	Adult	Adult
Susie <sup>a</sup>	1982 <sup>b</sup>	F	4	Adult	Adult
Lady <sup>a</sup>	1982 <sup>b</sup>	F	5	Adult	Adult
Jimmy <sup>a</sup>	1979 <sup>b</sup>	M	6	Adult	Adult
Maiko	1984	M	7	Adult	Adult
Toby <sup>a</sup>	1979 <sup>b</sup>	M	8	Adult	Adult
Bila Isia	2001	M	–	Adol II	Adol II
JoT	2002	F	–	Adol I	Adol II
Gander	2003	M	–	Adol I	Adol I
Lola	2004	F	–	Juv	Adol I
Gilda	2006	F	–	Juv	Juv
Jerry	2008	M	–	Juv	Juv
Mary Rose	2010	F	–	Inf	Inf
Wilbur	2010	M	–	Inf	Inf

<sup>a</sup> Wild caught individuals

<sup>b</sup> Estimated birth year

‘discontinued’, where the actor ceased harassment immediately after the initial response of the target. Initial response to harassment was scored as the first type of behavior exhibited by the target in response to receiving harassment. If no response was recorded within 10 s of the onset of harassment behavior, then ‘ignore’ was scored as the initial response (Adang 1984).

## Data analyses

### Frequency analyses

Frequency data were compared using *G* Tests of Goodness of Fit with Williams correction applied ( $G_{\text{gof}}$ ) and *G* Tests of Independence ( $G_{\text{toi}}$ ) (Sokal and Rohlf 2012). Expected frequencies ( $E_{\text{freq}}$ ) of harassment and response behaviors were calculated by dividing the number of individuals in a given age and/or sex class observed performing the behavior ( $N_c$ ) by the total number of individuals in a given age and/or sex class ( $N_t$ ) and multiplying this number ( $N_c/N_t$ ) by the total number of behaviors recorded ( $B$ ):

$$E_{\text{freq}} = (N_c/N_t) \times B.$$

### Rank analyses

Pearson correlations were used to test rank effects and correlations between recorded behaviors. Dominance rank

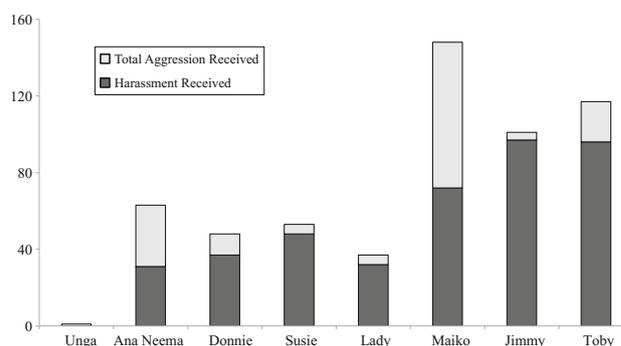
among adults was determined from the direction and outcome (e.g., fleeing upon aggression) of a decided agonistic event and displacement matrix and analyzed using R (version 3.3.1). Linearity in the dominance rank of adults was found to be complete and significant (Landau’s  $h = 0.476$ ,  $p < 0.01$ ). Individuals were, therefore, ordered into a linear dominance hierarchy and assigned a unique rank number where 1 represents the highest-ranking individual and 8 represents the lowest-ranking individual (Table 1).

All immatures had mothers in the group and some females had >1 immature offspring. The amount of harassment behaviors performed was averaged across all of a female’s immature offspring (for females with >1 immature offspring) in order to investigate the relationship between harassment performed and dominance rank of the actor’s mother. All other analyses were run using BIOMstat (version 3.30t).

## Results

### General pattern of harassment in bonobos

A total of 1140 agonistic events between all age-sex classes were recorded during the 2011 and 2012 seasons and 489 of these events were between an immature and an adult. Of these, 413 immature-adult agonistic events fulfilled the specific definition of harassment, given by Adang (1984) and described in the introduction of this paper, and were therefore classed as harassment by an immature toward an adult (Fig. 1). Of the 413 harassment events, 279 were categorized as ‘mild aggression’ and 134 were categorized as ‘physical contact aggression’ (Table 2). Harassment escalated into a conflict between the actor and target in 14 of the 413 recorded events.



**Fig. 1** Distribution of total aggression and harassment received by target

**Table 2** Distribution of type of harassment behavior received by sex of target

Type of harassment behavior	Target sex	
	Male	Female
Mild aggression		
‘bluff-like’	94	38
‘swinging object’	72	13
‘throwing object’	52	10
Total	218	61
Physical contact aggression		
‘bite’ ‘hit’ ‘kick’ ‘pull hair’, etc.	84	50
Total	302	111

### Actors

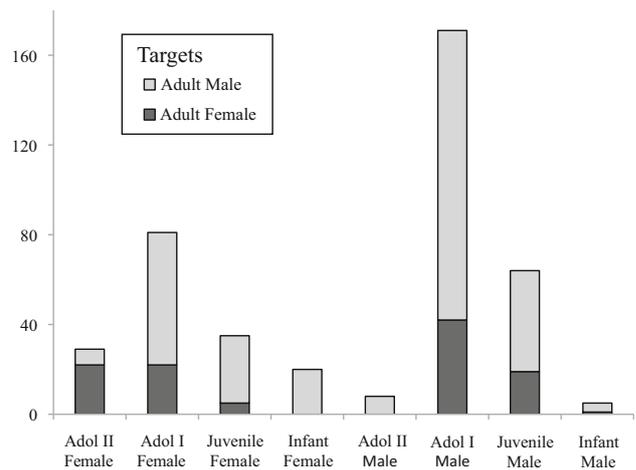
All immature individuals ( $N = 8$ ) were observed performing harassment behaviors, and there was no significant correlation ( $r = 0.384$ ,  $df = 3$ ,  $p = 0.190$ ) between harassment performed and dominance rank of the mother. Therefore, assuming an equal likelihood in performance, frequency of harassment did not show an expected distribution between the age or sex classes. Adolescent I performed harassment significantly more frequently than did adolescent II, juveniles, and infants ( $G_{\text{gof}} = 193.818$ ,  $df = 3$ ,  $p < 0.001$ ; Fig. 2; Table 3). We also found that males performed harassment significantly more frequently than did females ( $G_{\text{gof}} = 67.226$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 2).

### Targets

All adults received harassment from immatures with the exception of the alpha female (Unga). We could not fully test the prediction that immatures direct more harassment toward individuals outside of a ‘sub-group’ (as defined by Adang 1984) because all immatures had equal access to all the adults in the group and no adult females were observed engaged in allo-maternal care. However, immatures were never observed directing harassment behaviors at their own mother. For five of the eight adults in the group, harassment constituted the majority (>50% of the total) of aggressive initiatives they received (Fig. 1) and males were targets of harassment significantly more frequently than were females ( $G_{\text{gof}} = 91.674$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 2).

### Responses of adults to harassment

We found that the overall pattern of response to harassment did not follow an expected frequency distribution based on equal likelihood in type of response behavior. Agonistic responses occurred significantly more frequently than did neutral responses ( $G_{\text{gof}} = 34.737$ ,  $df = 1$ ,  $p < 0.001$ ). The

**Fig. 2** Distribution of harassment given and received by age-sex class

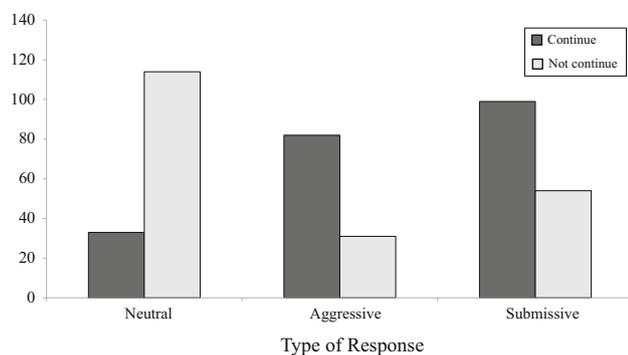
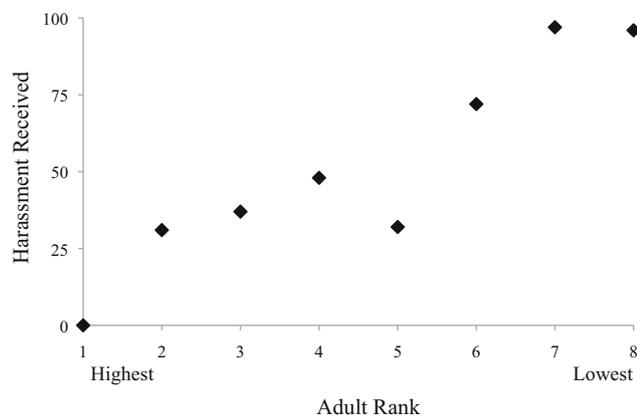
frequency of harassment received was significantly positively correlated with both aggressive ( $r = 0.771$ ,  $df = 6$ ,  $p < 0.01$ ) and submissive ( $r = 0.766$ ,  $df = 6$ ,  $p < 0.01$ ) responses, but there was no correlation with neutral responses ( $r = 0.089$ ,  $df = 6$ ,  $p = 0.236$ ). Continuation of harassment was found to be dependent on type of initial response, where both aggressive and submissive responses were followed by continued harassment significantly more frequently than were neutral responses ( $G_{\text{toi}} = 83.98$ ,  $df = 2$ ,  $p < 0.001$ ; Fig. 3). The type of response elicited was found to be dependent on the age class of the actor, where both adolescent I and II elicited agonistic responses significantly more frequently than neutral responses and both juveniles and infants received neutral responses significantly more frequently than agonistic responses ( $G_{\text{toi}} = 45.217$ ,  $df = 3$ ,  $p < 0.001$ ; Table 3).

### Rank effects

We found that the total amount of harassment each target received was significantly negatively correlated with target rank ( $r = 0.869$ ,  $df = 6$ ,  $p < 0.001$ ; Fig. 4). Furthermore, although no relationship was found between rank of the target and amount of neutral responses given ( $r = 0.020$ ,  $df = 6$ ,  $p = 0.732$ ), a significant negative correlation was found between rank of the target and amount of agonistic responses ( $r = 0.868$ ,  $df = 6$ ,  $p < 0.001$ ; Fig. 5). We also found that type of harassment behavior received was dependent on the target’s rank where high-ranking individuals received mild aggression significantly more frequently than physical contact aggression and lower-ranking individuals received physical contact aggression significantly more frequently than mild aggression ( $G_{\text{toi}} = 71.03$ ,  $df = 7$ ,  $p < 0.001$ ). The only immatures to elicit

**Table 3** Harassment performed and type of response elicited by age-class of actor

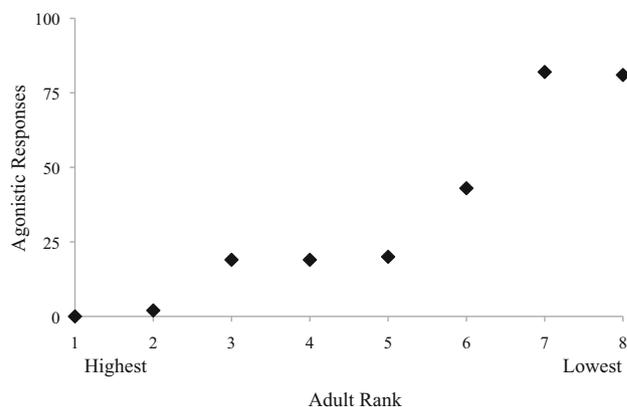
Actor age-class	Harassment performed		Response type elicited		
	Observed	Expected	Neutral	Agonistic	
				Submissive	Aggressive
Adol II $N = 2$	37	82.6	12	11	14
Adol I $N = 3$	252	123.9	61	124	67
Juvenile $N = 3$	99	123.9	58	16	25
Infant $N = 2$	25	82.6	16	2	7

**Fig. 3** Distribution of continuation of harassment received by type of response given**Fig. 4** Harassment received by rank of target

submission from adults during a decided non-harassment agonistic event were the two individuals classed as Adolescent II (Bila-Isia and JoT). Both Bila-Isia and JoT, however, continued to direct harassment behaviors at these lower-ranking adults (Maiko and Toby; Susie, Maiko, and Toby respectively).

## Discussion

The purpose of this study was to describe the pattern of harassment behavior in bonobos in light of two competing hypotheses (Exploratory Aggression and Rank

**Fig. 5** Agonistic responses by rank of target

Improvement) and to compare the results with those that have been reported for chimpanzees, a closely related species with both broad similarities in social system and key differences in dominance structure.

## General pattern of harassment in bonobos

Immature harassment of adults occurred frequently in this population of captive bonobos. The morphology of the behavior was similar to what was reported by Adang (1984) for chimpanzees, where individuals would aggressively pester an adult without being provoked and outside of the immediate temporal association of a conflict. The repertoire of harassment behaviors performed by immature bonobos was also similar to what was reported for chimpanzees (Adang 1984; Nishida 2003), varying from mild (e.g., throwing leaves) to more physical (e.g., kicking) types of aggression. Instances of harassment constituted roughly a third (36%) of all agonistic events recorded during the study period and represented the greater majority (84%) of those that occurred between immatures and adults. These events rarely escalated into a conflict but were a noticeable source of unrest within the group. Continued harassment of an individual responding agonistically, for example, would sometimes result in the group collectively moving to a new location within the enclosure or the separation of individuals into more diffuse spatial arrangements.

Adang (1984, 1985) reported that both male and female immature chimpanzees engaged in harassment behaviors in roughly equal frequency. Nishida (2003), however, observed that harassment was almost exclusively performed by immature male chimpanzees at Mahale and argued that harassment functioned primarily as a mechanism for immature males to gain dominance over adult females. More broadly, sex differences in the social interactions of immatures with adults (including aggressive interactions) has been documented in wild chimpanzees where male immatures interact more with adults than do female immatures and is in accordance with the documented sex differences in the social interactions of adults (Lonsdorf et al. 2014). We also found that while both the male and female immatures of our study population of bonobos harassed adults, immature males performed the behavior significantly more than did immature females. This result does, however, not agree with the observed interaction pattern of adult bonobos where adult females are known to interact frequently with both other adult females and adult males (White 1998; Hohmann et al. 1999). More detailed studies pooling all types of social interactions between immatures and adults and longitudinal studies following multiple immatures are needed in bonobos to fully understand this observation.

As discussed above, adult female bonobos can hold high rank positions (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016; this study) and it may be reasonable to expect that the offspring of high-ranking females would perform harassment significantly more than the offspring of low-ranking females because the threat of retaliation from the target is mitigated by the potential dominance asserted by their mother over the target. A somewhat similar effect is seen in species where female rank is inherited and matrilineal rank order is maintained through kin-based alliances (Chapais 1992; Chapais and Gauthier 2002) and there is evidence that the rank status of mothers can impact the relative rank status of their sons in bonobos (Surbeck et al. 2011). Surprisingly, we found that all immatures in this population frequently harassed adult group members, irrespective of their mother's rank, an effect that may be the result of the high levels of social tolerance that have been reported for bonobos (Hare et al. 2007; Hare and Kwtuenda 2010), although these findings on social tolerance have recently come into question (Bullinger et al. 2013; Cronin et al. 2015).

### Support for the exploratory aggression hypothesis

We found significant support for the Exploratory Aggression hypothesis (Adang 1984, 1985), which makes predictions about the generalized function of harassment

behavior as a means of social exploration. At Arnhem, Adang (1984) found that immatures directed harassment primarily at group members other than their own mother and the adult females that provided some allo-maternal care, individuals with whom they presumably had fewer opportunities to engage socially. Adult female chimpanzees at some field sites form close spatio-temporal associations (Wakefield 2013) but there is only limited evidence that they engage in allo-maternal care (Nishida 1983; The Jane Goodall Institute 2010; Kishimoto et al. 2014). Harassment, however, may still function as a way for immatures to reduce uncertainty when forming social connections outside of those associated with their mothers. Although the immature bonobos in our study population were never observed harassing their own mother, we were unable to test whether or not bonobos exhibit a pattern similar to chimpanzees (Adang 1984) because no adult females engaged in allo-maternal care during the study period. However, female bonobos are known to form strong and lasting social connections and actively maintain close spatio-temporal association in the wild (White 1996, 1998). Studies on adult female association patterns, allo-care, and harassment by immatures are needed into better examine this component of the proposed function.

The Exploratory Aggression hypothesis also makes predictions about the mechanistic properties of harassment and stipulates that the behavior will be most frequent when targets react in a way that reduces uncertainty by providing information about aggression and relationships between individuals (Adang 1985). We found that harassment would continue more frequently if the target reacted with an agonistic behavior than if they responded neutrally. These results support the hypothesis that agonistic responses are reinforcing in nature and are a mechanism through which immatures learn about the cause and effect of different agonistic behaviors and their relationship to the target (Adang 1984, 1985). Furthermore, when agonistic responses were separated into aggressive and submissive categories, both behaviors were correlated with frequency of harassment. This result is important because it demonstrates that immatures use harassment to explore both sides of agonistic behavior and not strictly as a tool of dominance or way to elicit submission from a target.

Adang (1985) also observed that the immature chimpanzees of Arnhem explored the differential effects of aggression across the dominance hierarchy by directing mild forms of harassment behavior at high-ranking individuals and more physical contact aggressive behaviors at low ranking individuals. He concluded that this behavioral pattern is less related to reducing uncertainty and is instead a reflection of immatures investigating the authority of high-ranking individuals and learning about the constituents of dominance as a behavior (Adang 1985). We

found a similar pattern of behavior in this group of bonobos, where high-ranking targets more frequently received more mild aggression and low-ranking received more physical contact harassment behaviors. Moreover, high-ranking individuals across species generally exhibit a high degree of social power (Lewis 2002) that can be used to insert force into inter-individual interactions (Flack et al. 2004). For example, although the highest-ranking individual in this group of bonobos (Unga) was never observed to be harassed, when provoked by group members in other contexts, her response behaviors were often highly aggressive and frequently resulted in the wounding of the potential aggressor, including immatures (Boose, unpublished data). Directing mild forms of harassment behavior towards high-ranking individuals is a way for immatures to reduce the potential risk of retaliation by exploring authority and the parameters of dominance from a distance.

### Support for the rank improvement hypothesis

We found mixed support for the Rank Improvement hypothesis (Nishida 2003), which makes predictions based on harassment as a mechanism of rank acquisition in immatures. At Mahale, Nishida (2003) found that harassment was primarily performed by immature males and was directed almost exclusively at adult females. Although he was unable to document this transition of power during his study period, he predicted that immatures would not harass adults once dominance over them had been established (Nishida 2003). During the course of our study period, two adolescent bonobos (Bila-Isia and JoT) began to ascend the adult dominance hierarchy, measured as an ability to elicit submission from adults outside of the context of harassment. Both Bila-Isia and JoT received submission signals from the two lowest-ranking adults, Maiko and Toby. JoT also received submission from Susie, a mid-ranking adult female in the group, but was never observed receiving submission from Jimmy or Lady, the two individuals ranking directly below Susie. However, because Lady is the mother of JoT it is likely that there was no opportunity to observe dominance interactions between the two. Maiko, Toby, and Susie continued to be able to elicit submissive responses from Bila-Isia and JoT and dominance between these adolescents and adults was, therefore, considered to be incomplete. Furthermore, both Bila-Isia and JoT were observed continuing to harass Maiko, Toby, and Susie after they successfully received submission signals from them.

Although we were not able to confirm the assumption that immatures will not harass adults they already out-rank, we found some support for the hypothesis that harassment functions to facilitate rank acquisition. In our study population, harassment received was negatively associated with the dominance rank of targets and low-ranking targets were

more likely to respond with agonistic behaviors. These results suggest that immatures are using harassment to ascend the dominance hierarchy and indicate that low-ranking individuals perceived harassment as a challenge to their rank status. In addition, adolescents were more likely to elicit agonistic responses from targets, and infants and juveniles were more likely to receive neutral behaviors in response to harassment indicating that targets viewed harassment differently based on the age-class of the actor and their potential ability to establish dominance over them.

The Rank Improvement hypothesis also predicts that responding to harassment with aggression will lead to the continuation of harassment whereas submissive responses will result in the cessation of harassment because submission indicates dominance over the target. We did not find support for this prediction. As stated above, we found that both aggressive and submissive responses were followed by continued harassment behavior from the immature. Although it is possible and likely that immatures are using harassment to acquire rank, these results more closely support the assumption generated by the Exploratory Aggression hypothesis that a primary function of harassment is to reduce uncertainty by affording immatures the opportunity to both control (i.e., elicit submission) and predict (i.e., elicit aggression) agonistic interactions.

### Further considerations

While there are broad consistencies presented in this paper, the patterning of harassment behaviors should also be expected to reflect a species' dominance and social structures. For example, female chimpanzees rank lower than males and are targets of harassment more frequently than are males (Adang 1984, 1985; Nishida 2003). Accordingly, the patterning of harassment and response behaviors should be different in bonobos in groups where females hold higher rank positions than males and/or where males occupy the lowest rank positions, as was the case in this study. We found that adult male bonobos were targeted more frequently than were adult females and reacted more agonistically to being harassed than did females, suggesting that male bonobos, like female chimpanzees, viewed harassment as a challenge to their rank status. These results are consistent with the different dominance structures of bonobos and chimpanzees and support the proposed function of harassment as a tool of rank acquisition.

The results presented in this paper, however, show that targets may not perceive harassment solely as a rank challenge and that harassment may not function the same during the course of development. The infant and juvenile bonobos of our study group received mostly neutral responses to harassment whereas the adolescents received mostly agonistic responses. In addition, the observation

that the alpha female, Unga, never received harassment demonstrates that immatures have some ability to assess the potential risk of different targets. Gathering information about and practicing aggression as an immature is important for later rank acquisition endeavors and to successfully function within a group. For example, in some species where rank is inherited, younger individuals use agonistic experiences with their peers to learn the fundamentals properties of rank acquisition as an adult (Holekamp and Smale 1991; Chapais and Gauthier 2002) as well as how to use allies to establish and stabilize the dominance hierarchy (Chapais 1988). Adang (1986) hypothesized that younger immatures may use harassment primarily as a mechanism to explore aggression whereas adolescents, who are engaged more in the testing and exploration of dominance, are using harassment primarily as a means to establish rank. Further studies tracking the development of immatures as they transition into the adult dominance hierarchy are needed to accurately test the prediction that the function of harassment changes as immatures age.

It is also worth noting here that, for five of the eight adults in this bonobo group, harassment constituted the majority (>50%) of aggression received during the study period. These five individuals were often observed responding in a manner consistent with the induction of a stress response (e.g., fleeing, screaming, fear grimacing). Although harassment of adults by immatures is a natural component of bonobo development, the effects of harassment are an important consideration for the management of stress in captive animals where it can be difficult for individuals to avoid each other or to remove themselves from the social situation.

## Conclusion

In conclusion, harassment is a distinct type of agonistic behavior that functions both as a mechanism of exploratory aggression and in a manner that facilitates rank acquisition. Our results on harassment behavior in bonobos provide support for several of the predictions generated by the Exploratory Aggression hypothesis and offer mixed support for the predictions generated by the Rank Improvement hypothesis. The results presented here also demonstrate that there are general patterns and broad similarities to harassment of adults by immatures between bonobos and chimpanzees, and emphasizes the need to examine this behavior separately from other types of immature-adult interactions in all species. At the same time, the comparison of bonobo harassment behaviors with those seen in chimpanzees shows that there are distinct patterns in choice of targets and the adults' responses that reflect differences that are consistent with each species'

social structure. Harassment is, therefore, an important part of the complex behavioral repertoire that immatures practice in order to become fully functioning and integrated members of their social group.

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## Compliance with ethical standards

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study protocol was approved by the University of Oregon Institutional Animal Care and Use Committee (IACUC). All data were collected using observations of spontaneous behavior at the Columbus Zoo and Aquarium (CZA), an Association of Zoos and Aquariums (AZA) accredited, and United States Department of Agriculture (USDA) regulated, institution in Columbus, Ohio, USA. CZA adheres to the welfare and husbandry standards outlined by the AZA and USDA.

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