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The Evolution of Pride: Do the Chimpanzee Bluff Display and Human Pride Expression Share Evolutionary Origins?

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A thesis submitted to the Faculty of Emory College of Arts and Sciences

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Abstract

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By Sara A. Price

Recent studies of pride suggest that it has a prototypical, universally recognized expression: a small smile with head tilted back, expanded chest, and arms akimbo or raised above the head. Primatologists have suggested that similar behaviors occur in the chimpanzee bluff display. This paper aims to assess shared evolutionary origins by comparing the morphological similarities between the chimpanzee bluff display and the human pride expression.

Data were collected from captive chimpanzees (*Pan troglodytes*) at the M.D. Anderson Cancer Center near Bastrop, TX. Each behavioral element included in a display was coded according to an ethogram, as well as the situational context in which the behavior occurred and whether display interactions resulted in the receipt of submissive behavior. A factor analysis was then performed on the data to reveal which behavioral elements co-occurred with the greatest frequency. The factor scores were saved and analyzed using Univariate ANOVAs to determine whether there were significant differences in the factor scores for behaviors across each social context.

The factor analysis revealed four factors, which we identified as different types of displays. The "bipedal bluff" (characterized by speed and intensity of raising two arms, bipedal running) was ubiquitous across all contexts. The "attack display" (one or two arms raised, hitting other individuals, jumping, running quadrupedally) was associated with dyadic interactions against females and was the only display type that received submission. The "pant hoot bluff display" (puckered lips, pout moans, rising and climax pant hoots, hitting inanimate objects) was associated with solo displays. The "aggressive bluff" (bulging lip face, hitting inanimate objects, intense stomping, jumping) was associated with group displays.

The combination of bipedal posture with arms raised, which loaded highly in the "bipedal bluff" and appeared in the "attack display," is similar to components seen in the prototypical human pride expression. These components are observed in contexts against females and elicit submission. Chimpanzees may use these behaviors to assert dominance and force submission on females, reinforcing status. Overall, these results suggest that a group of behavioral components found in the chimpanzee bluff display may have evolved into the human pride expression.

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INTRODUCTION

Emotion studies: past and present

Charles Darwin (1872) proposed the idea that emotions and their correlated expressions evolved through natural selection on the basis that certain observable emotions are automatic, shared by all humans across cultures, and may be homologous with similar states in other species. Furthermore, these emotions have adapted to serve biological functions related to needs that must be met for survival. A major finding in the early studies of emotions was the discovery of a small set of basic emotions that have distinct, universally recognized, nonverbal expressions - anger, disgust, fear, happiness, sadness, and surprise (Ekman & Friesen, 1971; Ekman, Sorenson, & Friesen, 1969; Izard, 1971). These findings were based upon studies demonstrating agreement across a range of nations and cultures, including isolated, preliterate tribal groups, on the emotions conveyed by each of their distinct expressions.

Much debate has surrounded the concepts of universality and "basic" emotions. Two theories have been suggested that account for universality (Matsumoto & Willingham, 2009). In one theory, individuals from different cultures learn to associate facial configurations with emotional states, using observational learning and reinforcement. Thus, facial expressions are universal because the same expression is modeled and observed around the world in response to the same situations. In another theory, facial expressions are a product of our evolutionary history, and are genetically coded in all humans, originating as an evolved emotion-response system. According to Ekman (1992), basic emotions are a distinctive class of psychological phenomena marked out by their automaticity, by unique behavioral and physiological signatures, and by the

existence of homologous states in other primates. Ekman (1999) has suggested an extended list of emotions, including pride in achievement. However, empirical evidence for more complex self-conscious emotions is lacking in humans, and even more so in nonhuman primates, whose behavioral expressions may share evolutionary origins with human emotional expressions.

Due to its positive valence (and the early assumption that all positive emotions share the same facial expression), as well as its complexity, pride expression has received relatively little empirical attention in the past, despite Darwin's claim that "of all the . . . complex emotions, pride, perhaps, is the most plainly expressed" (p. 263). Pride is defined as a self-conscious or social emotion that requires the capacity to reflect on one's thoughts and feelings, and accordingly, it is thought to be unique to humans and possibly great apes. Recent studies suggest that pride expression is associated with a stereotypical nonverbal expression, spontaneously displayed, and recognizable across cultures (Tracy & Robins, 2007a).

Pride expression

The most prototypical pride expression includes facial (low-intensity smile) and bodily components (expanded posture, slight head tilt, arms akimbo with hands on hips or raised above the head with hands in fists). Studies on the development of pride have demonstrated that preverbal toddlers show a specific set of nonverbal behaviors (smile, head tilted back), and three-year-olds additionally show erect posture (expanded chest, shoulders back), in response to success that is absent in scenarios when they fail (Lewis, Alessandri, & Sullivan, 1992; Stipek, Recchia, & McClintic, 1992). Moreover, this expression is reliably recognized and distinguished from similar emotions (e.g.,

happiness) by adults from several cultures, including a highly isolated, preliterate tribe in Burkina Faso, West Africa, as well as by children as young as four years old (Tracy & Robins, 2008; Tracy, Robins, & Lagattuta, 2005). It is especially unique because unlike basic emotions, it can easily be identified through both facial expressions (a small smile) and through the body, with expanded and upright posture, head held high and slightly tilted back, and hands on the hips or clenched fists raised above the head (Tracy & Robins, 2007b). The role the upper body plays in the expression of pride is especially important, because the emotion of pride shares similar facial expressions with other more basic emotions, such as happiness.

Pride expression has been shown to be spontaneously expressed in individuals in pride evocative experiences. Pride first emerges near the end of a child's third year, and children show some components after a successful encounter (Stipek, et al., 1992), as well as blind and congenitally blind athletes from over thirty nations competing at the Paralympic Games (Tracy & Matsumoto, 2008). On the other hand, there are likely cultural differences in the way that pride is expressed, based on cultural values. In a comparison between two individualistic cultures (United States and Australia) and two collectivistic cultures (China and Taiwan), pride was one of the few emotions valued differently across cultures. In the individualistic cultures, pride was more highly valued, while in the collectivistic cultures, pride was deemed undesirable (Eid & Diener, 2001). The differences found may be related to how pride is conceptualized. Tracy & Robins (2007c) have suggested two distinct facets of pride, an "authentic" pride and a more "hubristic" pride. "Authentic" pride may be positively correlated with self-esteem and function to promote future positive and pro-social behaviors, and therefore promote

status. "Hubristic" pride may be positively correlated with narcissism, and may alternatively promote aggression and hostility, and as a consequence, be less socially acceptable. It is possible that in collectivistic cultures, conceptualization of pride in individuals may be more similar to the "hubristic" facet of pride. Furthermore, since pride expression involves both facial and body components, it may be more flexible and easily regulated than an involuntary facial contraction seen in more basic emotions. This factor may be important in cultures where pride expression is not tolerated (Tracy & Robins, 2007a), and suggests that differences across cultures would be expected. Collectively, these studies suggest that pride expression has both biological and learned components. The expression may consist of similar core components across humans, which are then influenced by culture.

Pride, in its adaptive function to enhance the self, may be a behavioral type that has different meanings that are contextually derived. Cultural aspects may play a role in how pride is regulated, expressed, and experienced; however, several studies converge on the idea that the elicitors of pride expression (the evolutionarily programmed cognitive antecedents) and the adaptive outcomes are the same across nations and cultures (Tracy & Robins, 2007a).

From an evolutionary perspective, not only should humans show accurate and quick recognition of the particular emotion expressed, but they also should be able to decode what each expression means. Previous studies have concentrated mainly on the approach-oriented signals of positive emotions and the avoidance-oriented signals of negative emotions (Mogg & Bradley, 1999). Broadly speaking, emotions help facilitate appropriate responding to a range of context-specific situations. According to studies by

Tracy and Robins (2007a), the natural selection of self-conscious emotions serves two functions: "promoting the direct attainment of survival and reproductive goals, and promoting the attainment of social goals (e.g., getting along and getting ahead) which are more distally related to survival and reproduction." While basic emotions evolved primarily to promote survival and reproduction, self-conscious emotions like pride likely evolved to promote more social goals (Keltner & Buswell, 1997; Tracy & Robins, 2004b). The complexity of human social structures, which include overlapping and intransitive social hierarchies, likely selected for the ability to hold complex self-representations, and to use self-awareness to coordinate behavior to meet an ideal representation based on the values of society (Robins, Norem, & Cheek, 1999; Tracy & Robins, 2007a). Socially, pride is an emotion that reveals to an individual that he or she has done something that justifies a gain in self-respect regarding a position of importance or superiority. Moreover, the expression of pride "may serve a complementary adaptive function: alerting others that the proud individual merits increased group acceptance and social status" (2007a).

The actual expression of pride works to inform others that the individual warrants a beneficial reaction from others, through status and acceptance. In humans, high social status individuals are assumed by others to show more pride than lower status individuals when compared on the same task (Tiedens, Ellsworth, & Mesquita, 2000). However, in chimpanzees, social dominance is more flexible, depending on context and alliances, and so the same may not hold true.

Tracy and Robins (2004a; 2007a, 2008) have suggested possible functions for two components of the pride expression: expanded posture and a small smile. Expanded

posture allows the individual to appear larger, and larger body size conveys dominance and attracts attention. This allows for other individuals to recognize the individual at the opportune moment after an achievement. The small smile distinguishes it from a Duchenne smile elicited by happiness. The smile may also convey amiability after an achievement; without it, the expression may promote unwarranted hostility in response to a gain in dominance.

Homologous states

In his studies of emotions with universal expressions, Ekman (1999) emphasized the existence of homologous states in nonhuman primates as evidence that expressions are the product of our evolution and are shared by all primates. This was echoed by other researchers: "If expression is largely biological and innately determined, we should expect considerable similarity between ... two closely related species. If on the other hand culture is largely responsible for expression we should expect marked differences..." (Klineberg, p. 179).

Within the social communication of animals, ritualization refers to the changes in the signaling system throughout evolution, resulting in signals that are more effective in provoking appropriate behavior in another individual. The signals result from movements that have lost their original functions (Eibl-Eibesfeldt, 1989; Huxley, 1914). They are more stereotyped than the original movements, are more conspicuous and less ambiguous (Cullen, 1966; Huxley, 1914), and have evolved if they increase the transmission of reliable information (Zahavi, 1980). Although ritualized signals are uniform, they may be performed in different ways by different individuals, or in different contexts. This difference often shows the intensity of the signal (Zahavi & Zahavi,

1997), which could also be an indicator of fitness and how well an individual can handle handicap costs. Furthermore, slight individual differences in ritualized signals may be important for recognizing the identity of the signaler in animals with complex social relationships, such as primates (Cullen, 1966).

Signals are read by the observer as indicating a future behavior, so that appropriate action can be taken in advance. Forms of ritualized fighting, such as the bluff display, are adaptive in reducing the risk of injury to both winner and loser. It has been recognized that even in communication systems in which reliability of the signal is enforced by handicap costs, deception is possible only if there is a limit to the frequency of bluffing, so that the incentive for receivers to respond to the threat is not eliminated (Grafen, 1990). Deception is possible because it is costly for receivers of bluff displays to investigate in order to discriminate a bluff from a legitimate threat. Adams & Caldwell (1990) suggested that a variation in costs and benefits to different individuals could select for both reliable and bluff displays. Assuming that the benefits derived from a display are not the same for individuals of different fitness qualities, it is likely that weak individuals may benefit more from performing a bluff display (Adams & Mesterton-Gibbons, 1995). Less fit individuals may benefit more by bluffing to avoid conflict, in comparison to more fit individuals that are better able to fight if necessary, which would suggest that the pattern of threat displays may not be a reliable indicator of individual condition.

Using comparative studies, it is often times possible to trace the evolutionary history of a signal, and a signal shared by two species may indicate a common evolutionary origin. Most of our understanding of emotions in animals has come from

research in communication; what signals are used, how the signals are perceived by other individuals in the group, and the consequential effect on behavior. These signals are of special importance within nonhuman primates, due to the demands of living in a complex social environment.

Research has shown that the structures of a range of facial expressions are very similar among related primates, as well as humans, making them comparable across several species (Parr, Waller, & Fugate, 2005). Moreover, the fact that many of these same facial expressions shared among species are elicited in similar situations suggests a common function or meaning. For example, the silent bared teeth grin (fear grin) and the relaxed open mouth (play face) in chimpanzees have been shown to both encourage affinitive behavior between individuals (Waller & Dunbar, 2005). Van Hooff (1972) has argued that these chimpanzee expressions are homologous to the human smile and laughter, which also may have a similar function in increasing social bonding. Zivin (1977) has also described a "plus face" in children, with brows raised, chin elevated, and neck held firmly upright. It has been suggested that this face may act similarly to threat faces in apes, due to similar features of the "plus face" to threat faces in nonhuman primates, as well as a correlation between "toughness" rank and the number of "plus faces" given. While these expressions in nonhuman primates may not necessarily be attributed to specific emotions, like human expressions, they may be elicited by a similar internal state. Chimpanzees have demonstrated self-recognition in the mirror self-recognition tests (Gallup, 1970), which may imply that they have a level of self-awareness that would be needed to formulate self-representations.

Though pride has been thought to be unique to humans, evolutionary analysis requires investigation into our closest ancestors. Emotion has often been attributed as a phenomenon that underlies animal behavior. The behavior of chimpanzees, specifically through dominance or "bluff" displays, is strikingly similar to expression of pride in humans. Past studies have ventured into the possible evolutionary link between pride in humans and nonhuman primates: the fact that pride necessarily includes an expanded posture, is consistent with the suggestion that pride evolved to signal dominance, which is typically associated with largeness and a 'cocky,' expansive gait in nonhuman primates, such as chimpanzees (de Waal, 1989).

Understanding bluff displays within social context

A chimpanzee bluff display, often referred to as a dominance display or threat display, is a set of behavioral components frequently associated with agonistic encounters, but may also occur independently. They are often used by dominant chimpanzees for intimidation purposes. Although "bluff" gives the impression that it is undirected, bluff displays may be classified differently based on context. A pure bluff refers to a situation where an ape shows hair-erection and performs behavior elements of the bluff category (e.g. arm-swaying; stamping), but does not show towards, or receive from another individual strictly agonistic behavior (de Waal & van Hooff, 1981). A bluff solo occurs away from other individuals, a multi-directed bluff is aimed at multiple individuals simultaneously, and a bluff dyad is performed towards a specific individual (1981).

Studies of chimpanzees in the wild provide evidence of what displays look like and what they may mean. Goodall (2000) has cited behaviors such as charging, hurling

items, dragging and shaking branches, slapping and stamping the ground, and drumming. The displayer is also characterized with hair standing on end, and lips tightly compressed in a scowl. Vocalizations are also a defining feature in displays. A pant hoot is a loud individually distinctive call often used in agonistic displays to announce an individual's presence. Pant hoots vary from 2 to 23 seconds and have four different phases. The call starts with an introduction with unmodulated tonal elements, and then progressively builds up in volume, containing both inhalations and exhalations. A climax occurs, which resembles a scream, and the call ends with a "let-down" portion that has elements similar to the build-up (Marler & Hobbett, 1975; Mitani, Hasegawa, Gros-Louis, Marler, & Byrne, 1992).

Because chimpanzees live in a fission-fusion society, social relationships, especially between males, may be unpredictable since males break up into groups and may reunite as long as weeks later. Males are unable to monitor the flexible social organization at all times, and must constantly reassert their dominance through agonistic displays (Mitani, Watts, & Muller, 2002). Displays may also make the individual appear larger and more dangerous, and may intimidate rivals without recourse to aggression (Goodall, 2000).

Another important factor to consider is that formal dominance and success in agonistic encounters may overlap, but are quite distinct as well. The ritualized signals of chimpanzees are not agonistic in nature. A subordinate chimp may show a submissive display while a dominant moves an arm over the other's displaying body, but this is more often seen as greeting or during social excitement rather than during escalated aggressive encounters (de Waal, 1986).

Moreover, the ritualized submission display directed towards a bluffing dominant chimpanzee is an indicator that the bluff display is not simply an aggressive response that signals hostility. To an inexperienced observer, a chimpanzee's bluff display may appear to be merely an act of aggression. However, if this were the case, there would be a dispersive effect, and fear in the subordinate would drive the individual away completely without ever coming back. Submission, on the other hand, "is the effort of the inferior to attain friendly or harmonic social integration" (Schenkel, p. 319).

Present study's goals

In chimpanzees, bluff displays occur before or during agonistic encounters, while in humans, pride expression occurs after a successful encounter. If human pride expression evolved from earlier nonhuman versions in the form of dominance displays, we expect homologies of human pride in nonhuman primate displays in situations parallel to those that elicit human pride (Shariff & Tracy, 2009). The evolutionary analysis of pride, through the investigation of behavior in primates, particularly through bluff displays, can provide insight into the issue of why and how humans have evolved to express pride in such a manner.

The present study aims to assess the morphological similarities between bluff displays in chimpanzees and pride expression in humans. We predict that the bluff displays in chimpanzees and expressions of pride in humans are morphologically similar, suggesting that expression of pride in humans may have emerged from a basic set of behavioral elements found in bluff displays. Support for our theory would come from evidence of morphological similarities (similar components that signal emotion) between bluff displays and the human pride expression. Our first aim is to define which behavioral

components best define the bluff display and how social context interacts with them. Our other aim is to determine whether behavioral components are shared in common between the bluff display and human pride expression. We will examine these issues by coding the specific facial and bodily behaviors involved in each and conducting cross-species comparisons. We will also examine the behavioral components across situational contexts in which displays occur, and will observe and code the effect these displays have on others in the social environment.

METHODS

Subjects

Data were collected at the University of Texas M.D. Anderson Cancer Center near Bastrop, Texas, a facility containing 94 captive chimpanzees (*Pan troglodytes*).

Seven groups of chimpanzees at the M.D. Anderson Cancer Center were observed. Each group differs in the number of males and females (Table 1). The chimps range in age from juvenile to adult. Each group has an open outdoor enclosure (4500 ft^2) that connects to indoor sleeping quarters. The enclosures are all grouped together, so chimps from one group have limited visual access to adjacent groups. Each enclosure has a large climbing structure, with numerous enrichment items, such as plastic barrels, rubber tires, and plastic balls. Entry to and exit from the sleeping quarters may be restricted. Subjects were observed in both restricted entry and free range contexts, but I observed the subjects in the outdoor enclosure only.

Procedures

Filming of the chimpanzee behavior occurred on the roof that connected all of the groups. The chimpanzees were in view at all times while outside except when directly under the roof platform. Two behavioral methods were used - focal sampling, in which one individual was observed for a period of time and all behavior displays were recorded, and ad lib sampling, in which all bluff displays were recorded regardless of the individual doing them. No variables were manipulated.

A Canon video recorder was used to film bluff displays in different situational contexts (Table 2). Data collection consisted of four-hour long footage sessions every morning and afternoon for several days. The chimpanzees were given free access both inside and outside, and the groups were fed sporadically.

Analysis

Display behavior was isolated from the video footage using Adobe Premiere, categorized, and coded for behavioral items and situational context. We created an ethogram (Table 3), incorporating facial and body items, as well as different actions. A displaying individual was tracked until out of sight. Each behavioral element was coded for body actions, duration, and intensity. Longer displays that involved changing situational contexts were split up, so that a sequence corresponded to its different context. If a behavioral item was repeated within a single sequence, the maximum duration or intensity was scored. If there was an interruption in a behavior lasting longer than two seconds, it was considered to be a new bout, and the maximum score was counted. The situational context was coded as solo, group, or dyadic interaction (Table 4). A context was also coded based on whether the displayer received submission from another

individual. After categorization and coding for situational context (Table 2), a factor analysis was performed to assess the combination of elements that co-occur, and which elements best predict each category.

RESULTS

A total of 336 sequences from 40 different individuals (29 males, 11 females) were isolated from the clips. We eliminated individuals from the analysis with fewer than five display sequences, leaving us with 298 sequences from 20 different individuals (18 males and 2 females). We removed any behavioral item that occurred in less than five percent of the sequences (drumming, kicking, throw at, throw undirected, self-scratch, and clapping), and combined stomp with one foot and stomp with two feet. We also removed the speed, duration, and intensity scores for sway and swagger to eliminate possible clustering in the same factor that could be attributed to the items not being independent, e.g., a sway or swagger was always coded with a corresponding value of duration and intensity.

We performed a principle components factor analysis with varimax rotation on the behavioral item scores. The analysis revealed a total of 29 factors, but the first 4, as identified by the scree plot (see Figure 1), were the most significant, accounting for 35.29% of variance. We re-ran the same analysis, limiting it to 4 components. In defining each factor, we considered all behavioral components with a loading value > .25.

Factor 1, which we've named "bipedal bluff," is characterized by speed and intensity of two arms raised and bipedal running (long duration, many steps, and great speed). Factor 2, named "attack display," includes one arm raised, two arms raised (faster

and more intensely than in Factor 1), hitting animate objects (other individuals), jumping, and running quadrupedally. Factor 3, named "pant hoot bluff display," includes pucker lips, pout moans and pant hoots, and hitting inanimate objects. Factor 4, named "aggressive bluff," is characterized by bulging lip face (which is a threat face in chimpanzees), hitting inanimate objects, stomping, and jumping.

Next, to explore the relationship between these factors and different situational contexts, we ran univariate ANOVAs in which each factor score was the dependent variable and context was the fixed factor (Figure 2). The analysis revealed no significant difference in the Factor 1 scores across the four social contexts, $F(3, 294) = 1.33$, $p = .26$. There was a significant difference in Factor 2 scores across contexts, $F(3, 294) = 5.4$, $p = .001$. Factor 2 was most associated with dyadic interactions against females. There was a significant difference for Factor 3 scores across context, $F(3, 294) = 24.4$, $p < .001$. The behaviors in Factor 3 were most highly correlated with solo displays. There was a small significant difference in Factor 4 scores across contexts, $F(3, 294) = 2.7$, $p < .05$. Factor 4 was most associated with group displays.

We also ran a univariate ANOVA to assess when submission was received by the displayer (Table 5, Figure 3). Out of the 298 sequences, only 43 were followed by a submission. Factor 1 had no significant difference in submission across context. Factor 3, $F(1, 296) = 13.8$, $p < .001$, and Factor 4, $F(1, 296) = 10.7$, $p = .001$, loaded negatively with submission. Factor 2 had significant different (positive) factor scores when submission is received compared to not, $F(1, 296) = 19.5$, $p < .001$.

In order to ensure that our results were not a consequence of a single individual contributing considerably more than the other individuals to create a trend, we sorted by

factor and examined the spread of individuals with factor scores over 1. Since Factor 1 did not differ significantly across contexts, we only assessed Factors 2, 3, and 4. No single individual contributed over 50% within each factor.

DISCUSSION

In regards to our first aim, the study revealed several interesting findings about the structure of chimpanzee bluff displays and how situational context may influence what behaviors are displayed. First, the behavioral components observed by chimpanzees clustered into four factors. The distinct morphological combinations revealed in these factors allowed us to identify and name four different types of displays, a "bipedal bluff," "pant hoot bluff display," "aggressive bluff," and "attack display".

Second, with the exception of the "bipedal bluff" which was ubiquitous across all contexts, the other three display types were associated with distinct contexts. This evidence suggests that expressive behaviors differ depending on the type of social context. Therefore, we can examine each particular display within its associated context.

The "bipedal bluff" is characterized by bipedal running, with several steps, long duration, and high speed, as well as two arms raised, though not as quickly or intensely as observed in other factors. This display behavior did not differ significantly across contexts. The bipedal stance with both arms raised may contribute to a generalized expanded posture used by individuals in all contexts to make themselves appear larger and more threatening. The bipedal running may inhibit movement of the arms, affecting the intensity and speed of movement. However, since this behavior does not differ across contexts, it is more difficult to interpret.

The "pant hoot bluff display" is characterized by puckered lips, vocalizations (pout moans, rising pant hoots, and climax pant hoots), and hitting inanimate objects. It is most associated with solo displays. The puckered lip face is directly associated with the vocalizations, since both exhalations from the pout moans and the rhythmic breathing of pant hoots would require puckered lips. Vocalizations are an essential part of a solo display, allowing an individual to make its presence known and attract attention from others. Pout moans loaded especially high, since they often precede a bluff display, and may signal agitation or may be equivalent to a chimp "riling itself up" for a display. Pant hoots signal social excitement, and climax pant hoots are characteristic of displays (Goodall, 1986). Hitting inanimate objects, rather than actual individuals, is also characteristic of bluffs, and may function to create a loud intimidating noise while attracting attention. These combinations of behaviors all attract attention to an intimidating individual without the displayer having to direct a threat at a specific individual. This is reinforced by the high negative loadings of scream (-.336) and grimace (-.372), which would reveal fear in an individual and counteract the threat.

The "aggressive bluff" is characterized by the bulging lip face, hitting inanimate objects, stomping intensely, and jumping. This display is associated with group displays, where many individuals are displaying at the same time. The bulging lip face is a threat face in chimpanzees, described as Goodall (1986) as a "glare, prior to attack." Barking just barely missed our cut-off loading score (.249), however, it may still be relevant in that it may also be used as a threat in aggressive situations, described by Goodall (1986). As in the solo display, inanimate objects are hit rather than actual individuals, characteristic of a bluff. Stomping and jumping are also very intimidating behaviors.

Stomping had an especially high loading (.718), which may indicate a high level of social excitement. It is possible that since an individual's vocalizations are usually drowned out by other vocalizing group members within these group displays, other threatening behavioral items are accentuated.

The "attack display" yielded the most interesting results. This display is characterized by both one and two arms raised, hitting other individuals, jumping, and running quadrupedally. Bipedal run also just barely missed our loading score cut-off (.249), but is still relevant. This display is associated with dyadic interactions against females. One arm raised is especially quick and intense, and the raising of two arms is greater in speed and intensity than in the "bipedal bluff." Arm components, as well as jumping, may make the individual appear larger. Since this display is aggressive in nature, which usually includes hitting another individual, the quick and intense arm movements may be accentuated, especially in a female's presence. The quadrupedal running may be interpreted in different ways, either as a charge towards an individual before raising arms, raising arms and then running, or running past an individual after hitting in order to avoid retaliation.

Further, our analysis on submission behavior elicited by displays is also very revealing. "Attack display" was the only display that positively loaded with submission, while "aggressive bluff" and "pant hoot bluff display" loaded negatively. When context is considered, these results tell us that solo and group displays are not followed by submission. It is possible that the behavioral components within the "aggressive bluff" and "pant hoot bluff display" are more ritualized and may not signal as high of a motivation to attack, which would be characteristic of bluffing that prevents escalated

aggression. However, the behaviors in the "attack display" are used specifically by males to force females into submission, since there is very little risk of injury for a male.

In chimpanzee societies, different measures of dominance exist - a flexible layer of dominance, based on context, conflicts, and alliances, and a more stable formal layer of dominance, involving ritualized communication signals (de Waal, 1986). Within a hierarchy, there exist both dominance-related signals that express fixed positions, as well as outcomes of conflicts that are more variable and not fixed. Behavioral items such as arms above the head and bipedal posture may be more of a ritualized set of behaviors to make the displayer seem more intimidating. Because it was observed in all contexts, the "bipedal bluff" most closely represents classic ritualized display behavior. Other items, such as hitting and jumping, are aggressive, and are used as a way to indicate strength if a conflict were to escalate. Whereas the ritualized behaviors for intimidation may associate more with the flexible layer of dominance, behaviors included in aggression may relate more to the formal layer of more stable dominance, as indicators of inherent fitness in displayers. The "attack display" involved the combination of behaviors that elicited stereotyped submission, with crouching, bobbing, and pant grunting. Furthermore, this exchange of signals involved interactions against females, in which adult males outrank (Goodall, 1986; Nishida, 2003). Because there is little risk of injury, a male is more likely to use aggression against a female to force submission. Although there were 55 instances of dyadic interactions against males (almost the same number of instances as against females, n=54), none of the display types loaded highly with this context. The "attack display" had a much lower factor score for males than females. It is possible that

aggressive behavior against males is too risky, and that displays against males may depend more on the flexible dominance context that is not fixed.

The other main aim of this study was to compare the morphological similarities shared with the human pride expression. Within the four types of displays, our analysis revealed that there are behavioral components shared in common with the pride expression. In both the "bipedal bluff" and "attack display," we observed bipedal posture (expanded posture) with one or two arms raised. These components are consistent with the expanded posture and arms raised or akimbo present in the human pride expression. Therefore, these behavioral components that occur in both the bluff display and pride expression may share a common theme of making the individual appear larger. Moreover, in the "attack display," these behavioral elements are used by males to assert their dominance and force submission from females, which reinforces status in a way similar to how humans assert themselves through the pride expression after a successful encounter. Taken as a whole, the chimpanzee bluff display consists of a basic set of behavioral elements (mainly bipedal posture with arms raised) that the human pride expression may have evolved from.

Our results can be further applied to aspects of the human pride expression. We found both highly ritualized bluff display types across contexts, as well as more aggressive behaviors by males towards females that result in the receipt of ritualized submissive behavior. It has been suggested that pride may have two distinct facets, "authentic" and "hubristic" (Tracy & Robins, 2007c). "Authentic" pride may be positively correlated with self-esteem and function to promote future positive and pro-social behaviors, and therefore promote status. "Hubristic" pride may be positively

correlated with narcissism, and may promote aggression and hostility. The ritualized set of behaviors observed across all contexts may relate more closely to the concept of "authentic" pride and promoting status. On the other hand, the aggression observed in the "attack display" by males to force submission from females may relate more to "hubristic" pride, which has connotations of arrogance. Aggression is more likely to be observed against females, who can be forced into submission with few risks. Moreover, a male's dominance rank over a female is not affected by this behavior, and his aggression may indicate inherent fitness. Essentially, males can afford to "bully" females without any social consequences. However, as previously mentioned, aggression towards other males was not observed as frequently, possibly because it is too risky. Amongst males, dominance is not fixed and depends on many factors, so pure aggression may have severe social consequences. Future studies that assess fixed dominance ranks in chimpanzees in relation to bluff display behavior might provide further insight.

Table 1: Group Composition

Group Number	Number of Males	Number of Females
1	4	4
2	7	6
3	3	5
4	2	9
5	4	6
6	4	6
7	6	5

Table 2: Context Descriptions

Context	Description
Solo display	usually involved a longer display without any observable elicitor; not directed towards any specific individuals
Group display	more than 2 individuals displaying at the same time; behavioral components may be directed or not
Dyadic interaction towards female	behavioral components directed towards a specific female
Dyadic interaction towards male	behavioral components directed towards a specific male
Displayer receives submission	pant grunting at displayer, crouching or bobbing in front of displayer

Table 3: Ethogram

Behavioral Item	# times observed	Definition	Parameters
Facial Components			
Stare at chimp	80	Eye-to-eye contact; considered new staring bout only if eye contact broken by longer than 2 seconds	Duration
Grimace	34	Mouth may be closed or slightly open with lips withdrawn and mouth corners retracted; teeth exposed; may occur with screams (Parr et al., 2005)	Present/Absent
Bulging lips	29	Mouth closed with lips pressed together tightly and bulging out as if individual blowing air; no vocalizations occur. Individual stares ahead (Parr et al., 2005)	Present/Absent
Pucker lips	66	Lips are pursed with rounded mouth and lips pushed forward	Duration
Vocalizations			
Bark	11	Loud, sharp vocalization; can be high or low pitched	Duration
Scream	22	Loud, intense, high pitched; like "aach-aach" (Parr et al., 2005)	Duration
Pout moan	47	Short, hooting "oo .. oo" vocalizations; short hooting, all exhalation (Parr et al., 2005)	Duration
Rising pant-hoot	33	Rhythmic breathing with rising inhalations and exhalations, like "hoo-hoo"; no climax at the end (Parr et al., 2005)	Duration
Climax pant-hoot	30	Rising hoots with loud screaming climax at end, like "waaa" (Parr et al., 2005)	Duration
Arm Components			
One arm raised	30	Single arm raised with the palm towards another individual; intensity rating based on angle (arm at 90º angle and perpendicular to body = 3; arm straight above head = 5)	Intensity Speed
Two arms raised	16	Both arms raised; same ratings apply as one arm item.	Intensity Speed

Hit	24 anim 51 inan	Individual hits ground, object, or another individual	Intensity Inanimate/Animate
Drumming	---	Individual repeatedly hits object more than five times in a row	Present/Absent
Clapping	---	Individual claps hands together	Duration Speed
Body components			
Entire body sways left to right	120	Individual moves body back and forth. May occur quadrupedally or bipedally. Each way is counted (L-R-L-R = 4). Steps include lifting the foot off the ground; does not need to be forward motion. Does not include bipedal swagger, which is a separate item. Swaying is slower than in swagger and usually no forward motion	Number back and forth Duration Steps Speed of walk
Standing upright on two feet	145	Standing bipedally, with or without forward movement.	Duration Steps Speed of walk
Bipedal swagger	49	Quick side-to-side swaying while individual walks bipedally. Shoulders hunched, piloerection. Arms slightly raised by side; arms alternatively swing forward as individual sways. Each way is counted. Steps include lifting the foot off the ground; does not need to be forward motion.	Number back and forth Duration Steps Speed of walk
Stomp	32	Individual lifts and brings foot down forcibly, either quadrupedally or bipedally. Individual may jump and forcibly land; creates noise	Intensity Number of feet
Rock back and forth	34	Individual rocks in a forward and backward motion, either sitting or quadrupedally	Duration
Kick	---	Individual kicks wall or object	Present/Absent Number of feet
Push object	75	Individual pushes object on ground, or swings on rope while planted on ground and swaying	Duration

Throw object	9	Individual throws object, either directed at another individual or undirected	Intensity At individual/ Undirected
Jump	62	Individual jumps, either on the ground, or from one piece of equipment to another. Intensity based on force/distance/effort put into the jump	Intensity
Locomotion	151	Movement of individual quadrupedally. Rating of 1 is equivalent to a slight shuffle forward, while 5 is equivalent to a sprint or charge. Does not include steps taken while standing upright, swaying, or during bipedal swagger (coded in previous items)	Intensity
Rigid arms	36	Implies locomotion; arms are stiff and rigid while individual moves	Present/Absent
Self-scratching	---	Individual scratches self, as if it has an itch. Implies agitation	Present/Absent

Table 4: Frequency of Sequences per Context

	Solo	Group	Dyadic vs F	Dyadic vs M	Total
Males	142	40	52	54	288
Females	7	0	2	1	10
Total	149	40	54	55	298

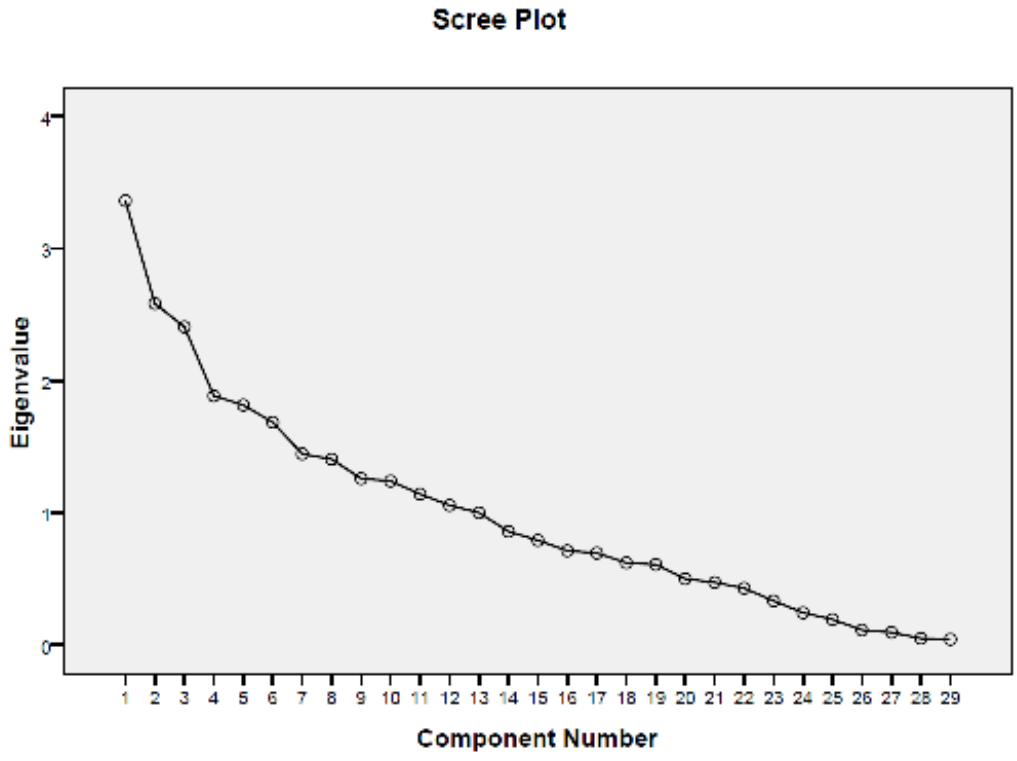

Figure 1: Scree plot of factor analysis results

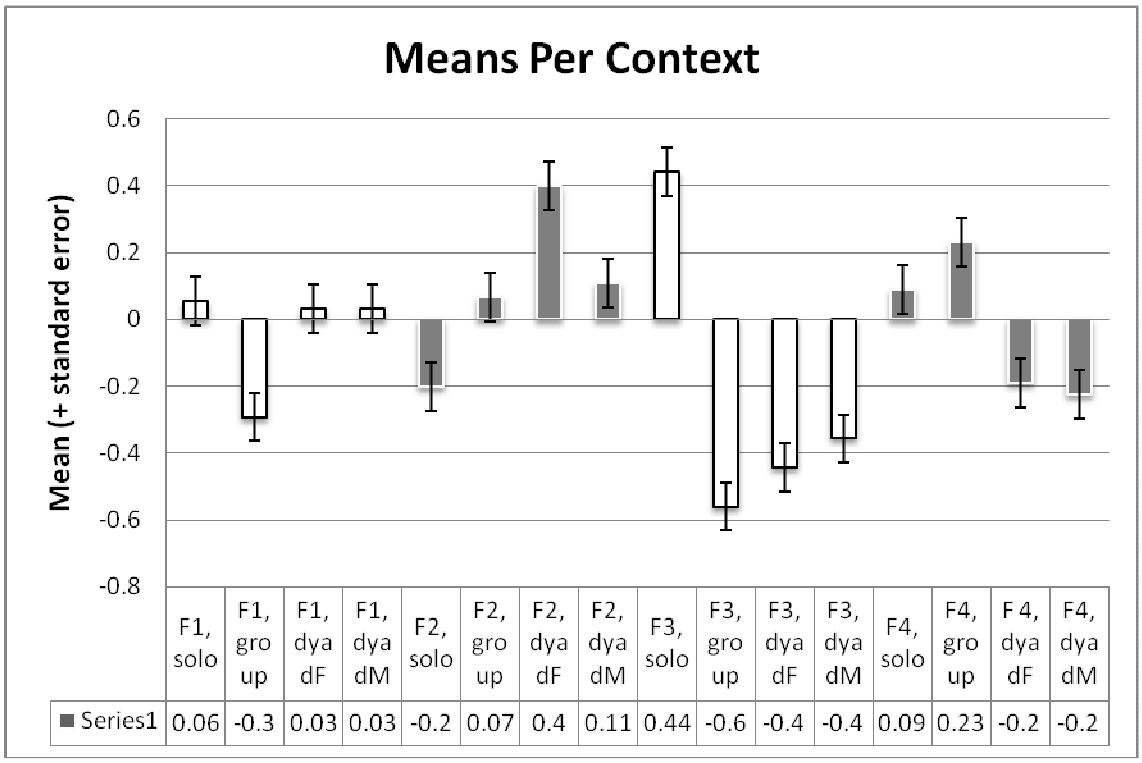

Figure 2: Mean scores of factors per context. Factor 1 did not differ significantly across contexts (p= .26). Factor 2 was associated significantly with dyadic interactions against females (p = .001). Factor 3 was associated significantly with solo displays (p< .001). Factor 4 was associated significantly with group displays (p< .05).

Table 5: Submission context across factors

	Factor 2		Factor 3		Factor 4	
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*
No submission received	-.102	.955	.086	1.03	.077	1.01
Submission received	.605	1.06	-.513	.593	-.454	.845

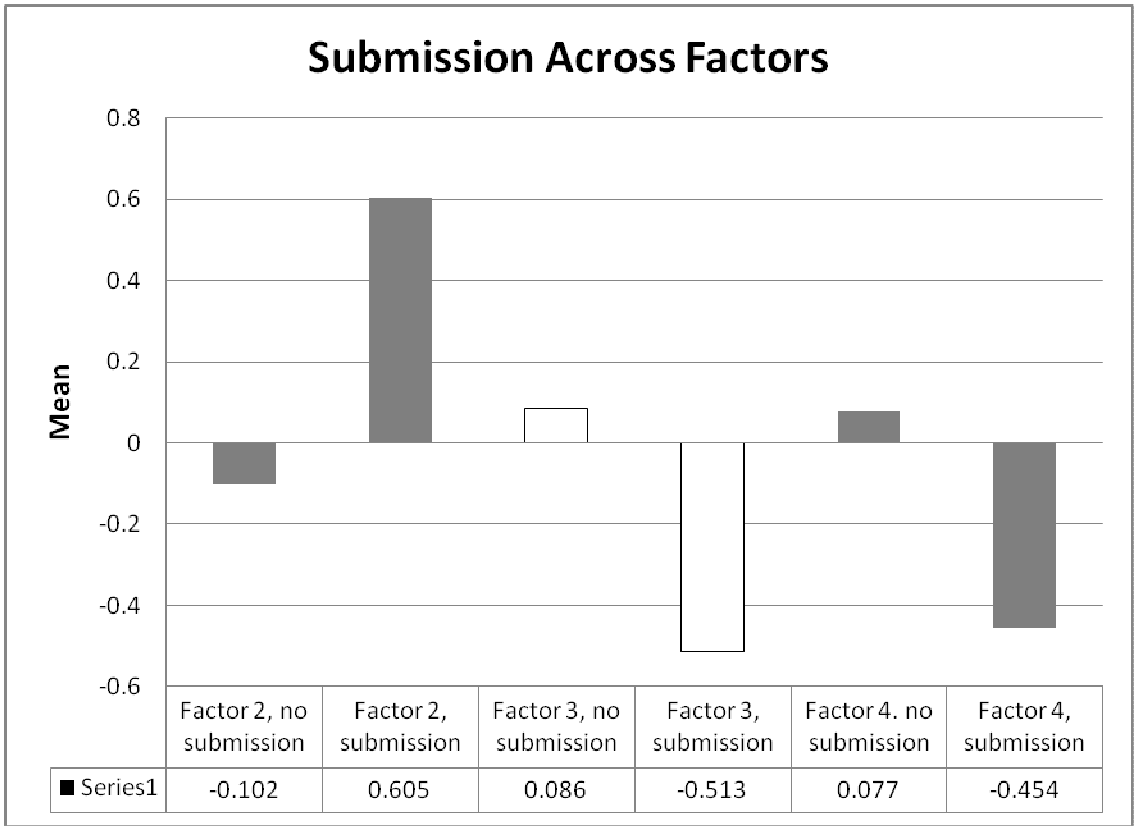

Figure 3: Representation of submission across factors. Submission associated positively with Factor 2 ($p < .001$), and negatively with Factors 3 ($p < .001$) and 4 ($p = .001$). Submission occurs after dyadic interactions with females, but not after solo or group displays.

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