Do Orangutans Really Laugh?

An Investigation into the Existence of Tickle-Induced Play Vocalizations among *Pongo pygmaeus* at the Orangutan Care Centre and Quarantine in Kalimantan, Indonesia

by

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Abstract

Laughter is a physiological process and a fundamentally social phenomenon with physical, biological, psychological, philosophical and social dimensions. Laughter is ubiquitous among human populations but its evolutionary history has not been thoroughly examined. Although laugh-like play vocalizations have been reasonably well-established among chimpanzees, little is known about its existence in other species.

It has been suggested from anecdotal reports on bonobos and gorillas, in addition to the handful of studies on chimpanzees, that play faces and play vocalizations are usually produced during rough and tumble social play and tickling. While there is a general consensus on the existence and characteristic features of great ape play faces, data on great ape play vocalizations and their relationship with play faces is scant. In addition, this limited evidence for laughter in great ape species does not extend beyond chimpanzees, and there has only been one other study conducted on orangutans thus far. This study tries to fill this void and investigates the existence of laughter in wild-born, ex-captive orangutans housed at the Orangutan Care Centre and Quarantine in Kalimantan, Central Borneo, Indonesia. Forty-one orangutan (24 males, 17 females) were tickled by familiar caregivers and their facial and vocal responses recorded. First, I analyzed the presence and frequency with which four play face variants co-occurred with vocalizations among the full sample. I then examined whether the reactions were influenced by sex, age, and time spent in rehabilitation. The analyses indicated that when tickled, orangutans exhibit play faces significantly more often than non-play faces and silent play faces more frequently than vocalized play faces. Sex, age, and time in rehabilitation did not affect these findings. Lastly, while some orangutans emitted vocalizations when exhibiting play faces, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. Therefore, the hypothesis that orangutans laugh could not be supported. Limitations of this study and future directions are discussed.

Keywords: orangutans; laughter; play vocalizations; play faces; tickling

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Chapter 1
Introduction

1.1 Thesis focus and structure

Laughter appears to be a human universal (Dunbar 2004; Eibl-Eibelsfeldt 1997; Ekman 1973; Provine 2000). There are three main reasons for thinking this. First, healthy adults in all cultures around the world laugh (Apte 1985; Darwin 1872; Luschei et al. 2006; McComas 1923; Provine 2000; Sroufe and Waters 1976). Second, laughter is one of the first spontaneous vocalizations to be emitted by human infants, appearing as early as four to five months of age, in the context of infant-caregiver interactions (Caron 2002; Sroufe et al. 1976). The third reason for thinking laughter is a human universal is that studies have shown blind and deaf children laugh in the same way as seeing and hearing children despite lacking visual and/or auditory cues (Darwin 1872; Eibl-Eibesfeldt 1970; Holland 1982; Sroufe et al. 1976).

Laughter has been found to have important social effects among humans. Studies have shown that laughter takes various forms and has various functions within conversation and other social activities (Bachorowski and Owren 1999; Glenn 2003; Provine 2000). It plays a central role in the creation, maintenance, and termination of interpersonal relationships (Bachorowski et al. 1999; Glenn 2003; Provine 2000). As a social lubricant (Dunbar 2004), it also eases tension, competition, and aggression, and stimulates playful interaction (Burgdorf and Panksepp 2006; Gervais and Wilson 2005; Panksepp and Burgdorf 2003; Van Hooff and Preuschoft 2003).

Laughter also has important effects on human health (e.g., Boston 1974; Gamble 2001; Martin 2002; Ostrower 2006; Provine 1996). Physiologically it increases adrenaline, heart rate and metabolism, and may even boost immune activity (Johnson 2003). It has also been shown to curtail negative emotions and stress and produce a general feeling of well-being. Thus, the general pleasure one feels from laughing also has actual physical health benefits that have the potential to enhance the survival and reproductive success of an individual.

Given that laughter is a human universal with important social and health benefits, it might be expected that its evolutionary history has been thoroughly studied. Such is not the case, however. The occurrence of laughter in the form of play vocalizations is reasonably well established in chimpanzees (Andrew 1963; Darwin 1872; Matsuzawa 2001; Plooji 1979; Provine et al. 2005; Provine & Bard 1994; Ross 2007; Van Hooff et al. 2003; van Lawick-Goodall 1968; Vettin et al.1999, 2005), but little is known about its occurrence in other species. To date, less than a dozen studies have systematically tested for laughter-like behaviour in species beyond the human-chimpanzee clade (Kipper & Todt 2002; Preuschoft 1992; Ross 2007; Vettin & Todt 2005).

With the latter point in mind, I investigated whether orangutans exhibit laughter similar to humans. I focused on orangutans for three reasons. First, they are one of the closest living relatives of humans and chimpanzees. According to recent studies (e.g., Britten 2002), the three species share more than 90% of their DNA. Second, studies carried out over the last 30 years have shown that orangutans share a number of complex cognitive and behavioural traits with humans and chimpanzees, including the ability to use and make tools (Galdikas 1982; van Schaik 2003), to engage in social learning (van Schaik et al., 2004), and even to acquire, use, and teach each other sign language (Shapiro 1982; Shapiro and Galdikas 1995). Given these similarities it seems reasonable to suppose that if laughter extends beyond the human-chimp clade, orangutans are one of the species in which it is likely to occur. Lastly, only one investigation of the occurrence of laughter in orangutans has been reported in the literature (Ross 2007) and this study has a number of important shortcomings.

This thesis has five chapters. In the remainder of this chapter I outline the generally accepted definitions and properties of laughter in humans. I then summarize the most influential theories on the origin and role of laughter in humans. I also discuss the meaning, function, and benefits of social play, tickling, and play signals among mammals since human laughter has been suggested to have evolved out of facial expressions associated with great ape social play and tickling interactions. Subsequently, I discuss current evidence for laughter in species other than *Homo sapiens*. Lastly, I outline the rationale and goals of the present study. The second chapter describes the methods I employed to collect data in the field, and the techniques I used to analyze the data in the laboratory. Chapter 3 presents my results. In the fourth chapter I interpret the results and discuss the major problems encountered with the research during both the data collection and analysis. I then outline what I think needs to be considered in future research. The fifth and final

chapter presents the conclusions I reached in the course of my study with particular emphasis on the contribution my study makes to the understanding of the evolutionary history of laughter.

1.2 Definition and properties of laughter

A smiling face is often referred to as laughter, and although they share similar characteristic facial features, laughter contains a vocal element which may be entirely absent in a smile (Provine 2000). According to Merriam-Webster's (2013) Dictionary, laugh as a verb is, "to show emotion (as mirth, joy, or scorn) with a chuckle or explosive vocal sound; to find amusement or pleasure in something; to become amused or derisive; to be of a kind that inspires joy."

As a bodily phenomenon, laughter is also relatively easy to describe (Holland 1982). It involves spasmodic contractions of the facial muscles, a brightness of the eyes, an open mouth, and bared teeth (Darwin 1872; Hertzler 1970; Boston 1974; Holland, 1982). In addition to these facial features, laughter includes a sudden relaxation of the diaphragm, quick, jerky expulsions of breath and the production of inarticulate sounds (Luschei et al. 2006; see Provine 1996; Trumble 2004).

Sonically, human laughter has distinct features that allow for its identification and evaluation (Kipper & Todt 2003; Provine 1996, 2000). This signature is characterized by four qualities: note structure, note duration, internote interval, and decrescendo. Laughter contains short, vowel-like blasts (1/15 of a second long) that are repeated at regular intervals every 1/5 of a second. Although a specific vowel sound does not define laughter per se, similar vowel sounds (e.g., he-he, ha-ha, ho-ho) are typically used. These blasts have a strong harmonic structure, decrease in pitch and intensity over time, and have a reversible quality causing the laugh to sound similar when played backwards. For Provine (2000), the most critical information is carried in the laugh notes and the time interval separating them—the so-called "internote interval". For example, it is difficult to laugh naturally with abnormally long or short note durations. Likewise, Provine (2000) argues that note durations with abnormally long or short internote intervals do not occur.

Laughter researchers argue that two forms of laughter should be recognized: Duchenne laughter and non-Duchenne laughter (Gervais and Wilson 2005; Keltner and Bonanno 1997). Duchenne laughter is emotional, spontaneous, involuntary, and genuine. It is sometimes referred to as proto-humour, and is thought to be the innate

and stimulus-driven form of laughter. In contrast, non-Duchenne laughter is conscious, strategic, voluntary, and artificial (Gervais et al. 2005; Provine 2000; Ruch et al. 2001). Non-Duchenne laughter can be fake or cruel as when people laugh “at” rather than “with” someone, and it is believed to develop with age, language, and cognitive maturity (Gervais et al. 2005; Provine 2000).

1.3 Theories about the origins of laughter

The origin and functions of laughter have long fascinated philosophers, psychologists, biologists, and anthropologists. The major hypotheses can be divided into early and current theories. The early theories comprise of 1) those that were proposed when academics based their hypotheses on general observations and philosophical reasoning (Ekman 1997); and 2) those that are based on ethological studies that emphasize laughter’s biological or adaptive roots. The most current theory holds that laughter originated in social play.

1.3.1 Early theories

Based on observation and philosophical reasoning

The earliest theories generally covered two main themes: laughter as the original expression of happiness, joy and high spirits, and laughter as an aggressive and intimidating vocalization used to collectively threaten a common enemy (van Hooff et al. 2003).

Charles Darwin was a major proponent of the first of these theories. He felt that the most common cause of laughter is the incongruous or unaccountable, something that excites surprise and a sense of superiority in the laugher. Darwin saw laughter as the natural and universal expression of joy or happiness (1872). His theory argued that smiling is the first stage in the development of a laugh, both of which signal amusement. Further, Darwin suggested that laughter is the opposite of the cries and screams of distress (Boston 1974; Darwin 1872), although they both serve equally well to expend superfluous nervous energy and can be employed in a forced manner to conceal another state of mind (e.g., anger, shame, or shyness).

Thomas Hobbes, Henri Bergson, and Sigmund Freud are among the theorists who discussed the second more aggressive theme. According to Thomas Hobbes

(1840), the two main elements of laughter are those of superiority and surprise. He emphasized the aspect of laughter that gloats maliciously and aggressively over others, and reduced laughter to a sudden expression of glory or celebration of self-importance (Boston 1974).

Henri Bergson (1956) also argued that laughter is aggressive. He explained the laughable as being based on incongruity. But for him it also had a useful social and evolutionary function as a social gesture and a form of rebellion against the mechanization of human behaviour and nature. Bergson saw laughter as the tool by which society corrected aberrant behaviour. This was done by means of humiliation in order to preserve itself from the deadening effects of political, ideological, social and psychological rigidity.

Sigmund Freud's (1928) theory was more complex than the others as it took into account two factors that are often separated and treated as exclusive: the offensive release of aggression and hostility, and the defensive protection of pure pleasure, joy, or play. Freud saw humour as being aggressive and arising from feelings of superiority, with laughter being the socially acceptable means of dealing with pain, releasing tension, and gratifying repressed sexual pleasure, hidden desires, and inhibitions.

Based on ethological studies

The second group of earlier theories on laughter is derived from ethological studies that emphasize laughter's biological basis. The first of these theorists is Irenaus Eibl-Eibesfeldt (1970). He writes of laughter in terms of an innate ritualized threat. This notion is based on the fact that when social animals jointly threaten an enemy, many primates emit rhythmic and aggressive vocalizations while simultaneously revealing their teeth. He argues that because laughter shares these elements and has a similar cohesive effect in humans that it probably originated in the aggressively motivated behaviour called "mobbing" (Boston 1974; Eibl-Eibesfeldt 1970). This idea is partially supported by Anthony Ludovici (1932) who points out that laughter gives the symptoms of an enraged animal, suggesting a primeval origin in the "showing of teeth" as an indication of challenge or threat.

The second theorist in this period is Konrad Lorenz (1963). Lorenz saw laughter as a form of joint aggressiveness against outsiders while simultaneously producing a strong bond of fellowship among participants. He, too, considered laughter to have likely evolved through the ritualization of redirected threatening movements.

However, in contrast to Eibl-Eibesfeldt and Ludovici, Lorenz felt that in its original form human laughter was also an appeasement or greeting ceremony, analogous to those observed in geese and dogs who break into extensive greeting when an unpleasantly tense conflict situation is suddenly resolved. In Lorenz' theory, smiling and laughing represented different intensities of the same behaviour pattern, responding with different thresholds to the same stimulus. Similar to other appeasement rituals, laughter contains a large measure of aggression directed towards nonmembers of the group. As a result, laughter is exhibited to divert such aggression and to create bonds and a feeling of social unity. Lorenz concluded that the original, and in many cases, the chief function of greeting rituals shared among animals, including laughter, is the prevention of fighting.

Also within this time period is a third theory by Desmond Morris suggested that smiles and laughter evolved from crying (1967). He describes them as having similar physical characteristics: musculature tension accompanied by a reddening of the head, watering of the eyes, opening of the mouth, pulling back of the lips, exaggerated breathing with intense expirations and, the high-pitched rasping vocalizations (Roeckelein 2002). Morris believes that when a child recognizes its mother, it gives a response that is half crying and half a parental-recognition gurgle. The combination produces a laugh but has since evolved to become fixed and fully developed as a separate, distinct response in its own right. He goes on to add that as adults, humans signal the people they meet to reveal that they are not aggressive but mildly apprehensive and rather friendly and attracted. He concludes that while it is possible for laughter to be both a potent social weapon and a play signal, it essentially conveys the message, "I recognize that the danger is not real."

1.3.2 Current theory

The above early theories suggest that laughter can be aggressive and intimidating, whereby the act of baring one's teeth is used and perceived as a joint threat or social weapon against outsiders. However, laughter has also been identified as an expression of happiness, joy and amusement that can be employed to consolidate alliances, maintain relationships, and create a sense of social unity and fellowship among participants. Therefore, as a social and gestural tool, it can be used to prevent fighting by designating behaviours as playful.

Social play and tickling theory

Today, it is the more commonly accepted hypothesis that the evolution of laughter originated with social play and tickling. Like laughter, the role of play in evolution is by its very nature, complex and hypothetical (Bateson 2005). One of the main problems with its study is the fact that there have been disagreements on its precise meaning. However, play manifests itself behaviourally in similar ways across many mammalian species (Pellegrini and Smith 2005) and is characterized as having the following features: threats are absent or infrequent, movements are free and easy, muscle tone is relaxed, biting is inhibited, roles frequently reverse, dominance of relations are relaxed, and sequences of behaviour vary (Aldis 1975). On the surface, this characteristic behaviour appears to be agonistic but it occurs in a non-serious and playful atmosphere (Fry 2005).

The term play has been applied to behaviour in animals that often resembles "real" behaviour but lacks, or cannot be seen to have, any immediate or normal biological consequences (Bateson 2005). The implication is simply that because it does not contain any obvious survival value, animal play cannot be serious, since if it were—if it had a function—it would then not be play (Loizos 1969). However, play has real biological costs (Bateson 2005). Animals expend more time and energy, and expose themselves to greater risks of injury and predation when they are playing than when they are resting, making them more conspicuous and less vigilant. However, the costs of play must be outweighed by its benefits. If play were functionless, those animals that played would be placed at a disadvantage compared to those who did not and play behaviour would not have evolved (Bateson 2005; Bjorklund and Pellegrini 2002; Loizos 1969). Due to the fact that social play is a ubiquitous mammalian characteristic (Bjorklund and Pellegrini 2002; Poirier et al. 1974, 1978) it seems highly unlikely that it would be so prevalent if it did not contribute to individual survival and reproductive success (Fry 2005). From this perspective, play can be argued to aid in the development of innovation, social affiliation, dominance hierarchies, communication, cultural transfer, and cognitive capacities (Lewis 2005) that benefit both the individual and the group.

At the level of the individual, play has both immediate and delayed benefits (Palagi and Paoli 2008). Play may typically prepare individuals for later adult behaviour (Bateson 2005) but it is also critical to childhood (Pellegrini and Smith 2005). Play offers an opportunity for physical stimulation which is necessary for proper development of muscle tissue, skeleton, as well as the development of those motor skills like running, climbing, grasping, and manipulation, all of which are essential for

survival (Loizos 1969; Martin and Caro 1985; Poirier et al. 1974, 1978). Play also aids in the formation of perceptual skills and enhances neural development by stimulating the central nervous system (Lewis 2005; Poirier et al. 1978). Thus, play helps to permanently mold individuals' physical, neural, and mental processes (Bjorklund and Pellegrini 2002; Lewis 2005).

At the social level, play helps individuals learn the skills and behaviours they need to become functioning adults. Through play, they can safely experiment with skills that involve testing boundaries and establishing themselves in the dominance hierarchy. This allows individuals to gain experience and become familiar with dominant and subordinate roles as they learn behaviours that will most likely characterize their relations with others for much of their lives (Poirier et al. 1974, 1978). Through play, individuals learn the maintenance of peer integration, social communication, and ultimately the entire socialization process (Poirier et al. 1974, 1978). Play fighting, wrestling, chasing and other playful behaviours provide practice and test the limits of the young's own strength, agility, social placement, and playful deception against its peers (Lewis 2005). Lastly, play serves to fully acquaint an individual with its species-specific and perhaps group-specific communication system.

It is precisely within this communicative repertoire that play signals fall (Bateson 2005; Poirier et al. 1974, 1978). These specific play signals include movements, gestures, facial expressions and vocalizations, and are a critical component of mammalian play. This is because social play always involves the potential for true aggression where the lines between play and actual fighting become blurred (Loizos 1969). In a basic play-chase, the initiator may approach another individual with characteristic traits: a bouncy gait, bobbing head, avoided gaze, a play face, and often quiet guttural vocalizations are exhibited (Loizos 1969). Agonistic signals can occur during play fighting, rendering the distinction between play and other behaviours that much more difficult to recognize (Bekoff 1975; Bekoff and Allen 1997). However, two animals engaged in a bout of wrestling have a relatively automatic or instinctive ability to recognize a playful interaction as such (Lewis 2005). Thus, it seems that it is not so much the actual behaviour patterns that are used but the way in which they are performed that is critical. Because it would be risky for an animal to misinterpret the intention of a behaviour, play signals have evolved to distinguish the serious from non-serious, allowing an appropriate and constant response from another individual (Allen and Bekoff 1994; Bekoff et al. 1997). In fact, it has even been argued that the ability to interpret ambiguous social cues could be one central component in

the evolution of behavioural flexibility and intelligence in primates (Bekoff et al. 1997; Pellis & Pellis 2007).

The elements of play signals we see today in the great apes are assumed to have originated with a common great ape ancestor (Andrew 1963, 1972; Darwin 1872; Fry 2005). This is because all of the great apes—humans, chimpanzees, bonobos, gorillas, and orangutans—share an ability, need, and desire to play. In addition, they denote a readiness to play in a similar manner, by exhibiting certain bodily postures, movements, and facial expressions.

Some researchers warn of the problems associated with ethological studies of nonhuman primate facial displays because of inherent imprecision when making comparisons among species (Chevalier-Skolnikoff 1973). However, according to Van Hooff (1972) and Ekman (1973), there is definite continuity and a progressive elaboration of facial expressions in taxa. A number of studies have been performed in which the repertoire of primate displays, particularly their facial expressions, have been described (Andrew 1963; Van Hooff 1972, 2003). In terms of the facial expressions connected to the smile and the laugh, the traditional scientific view, the "diminutive hypothesis" (Preuschoft 1994, 1992), considers them to be expressions of similar motivation and emotions (merriment and joy) that simply vary in intensity. Thus, some (e.g., Darwin 1872; Hayworth 1928; Koestler 1949) view the smile as a subdued, low-intensity, diminutive form of the laugh (Van Hoof et al. 2003; Preuschoft 1994, 1992). However, a comparative evolutionary approach based on investigations on chimpanzees and humans suggests otherwise.

Today, the generally accepted theory states that while in humans, laughing and smiling converged and eventually overlapped forming a single facial display, the comparative evidence suggests that they have completely different phylogenetic origins (Trumble 2004; Van Hooff 1972, 2003; Preuschoft 1992, 1994). This theory proposes that smiling is homologous to the "silent bared-teeth" (SBT) display that is found in monkeys and apes and is used to signal submission, assurance, affiliation and appeasement (Van Hooff 1972). It is said to be a ritualized low-intensity version of the "bared-teeth scream display" by which almost all species of primates express strong terror, fear and frustration. The message it sends is one that attempts to negate aggressive intention and can have an appeasing effect on a potential aggressor (Van Hooff 2003). Van Hooff (2003) concludes that the silent bared-teeth display, especially the confident, friendly form, has much resemblance to the emphatic greeting broad smile of humans. The latter can be a manifestation of friendliness but it is also a clear signal of submission and anxiety (Ekman 1973; Van Hooff 2003).

For humans, smiling is often an expression of attachment and friendliness signaling an affectionate attitude and positive intentions. However, a smile can also represent uneasiness with an ambiguous social situation and a desire to overcome the problem. This is also the case with the silent bared-teeth display exhibited by monkeys and apes (Van Hooff 1969, 1972). Smiles, then, are profoundly conflicted facial gestures, expressive of a willingness to be friendly yet associated with atavistic displays of teeth as weapons (Preuschoft 1992; Van Hooff 1969, 1972). Smiling as a sign of either dominance (threat display) or subordination (appeasement gesture) indicates a readiness of one individual to move toward another. This is done without intending to cause physical harm even though the baring of teeth and a close approach are also movements that could precede actual fighting. As a result, individuals must be able to discriminate among the different types of smiles to determine whether the motivation behind the expression is a friendly or hostile one (Caron 2002).

Human laughter, on the other hand, is said to have its roots in the original play face known as the “relaxed open-mouth” (ROM) display (Van Hooff 1972; Van Hooff et al. 2003). Like smiling, the ROM emerged from agonistic behaviour or from ambivalence and conflict on some level (Van Hooff 1972; Van Hooff et al. 2003). While the SBT display occurs in ‘serious’ competitive situations, the ROM display is restricted to playful interactions (Preuschoft 1992). These are said to have developed out of the intentional and protective movements of play biting, one of the foci around which play revolves. Initially, these movements of the facial muscles and mouth probably had biologically functional significance. Over time, however, they became exaggerated and developed greater emotional and communicative value (Gamble 2001) which would have been preserved because of their useful purposes: control of conflict at transition points, as a social lubricant to ease friction within the group, and to express tolerance for the ambiguity of mock-hostile play (Caron 2002; Van Hooff et al. 2003).

Although the interests of any two individuals engaging in social play will rarely coincide, competition has to remain inconspicuous. This is why the play face has an important function used to clarify that the ambiguous and potentially aggressive movements in play are just that — play (Bateson 2005). It sends the message, “we just pretend this was fighting” (Bekoff 1975) and should not be taken seriously. This demonstrates that the seemingly chaotic and unpredictable character of play is only possible by virtue of these specialized play signals that allow the rules to be broken (Bateson 2005).

Today, all of the great apes, including humans, have a select number of specific facial displays they employ during social play. Referred to as “play faces” these are meta-communicative expressions that basically differ in the degree of teeth-baring (Van Hooff et al. 2003), designating the behaviour with which they are associated as mock aggressive, playful, and enjoyable (Preuschoft 1995; Van Hooff 1972, 2003; Van Hooff et al. 2003). These faces are described as having the following characteristics: jaws widely open, mouth corners normal or slightly retracted, upper lip either covering the teeth (ROM) or exposing the upper teeth (OMBT), lower lips loose with the lower teeth exposed, raised eyebrows and eyelids, and a brightening of the eyes (Chevalier-Skolnikoff 1973; Darwin 1872; van Hooff 1972; Van Hooff et al. 2003).

In addition to the above facial characteristics, the play faces of humans and chimpanzees are accompanied by a staccato shallow breathing. Because this chimpanzee play vocalization closely resembles human laughter in both form and structure, several chimpanzee researchers (e.g., Darwin 1872, Foley 1935; Yerkes 1943; Goodall 1965; van Hooff 1967; van Lawick-Goodall 1971) have described this shallow breathing as soft, repetitive guttural sounds, low-intensity panting noises or play chuckles. This vocal component is a significant feature of human and chimpanzee play faces and it has been proposed that if it existed in our hominin ancestors, it would have reinforced the function of that display (Preuschoft 1995). That is, it would have signaled a playful mood like human laughter does today. This is because the mock fighting and wrestling in rough and tumble play can easily escalate to actual fighting and aggression if the friendly mood is lost. This volatile state is exactly why a play face and its accompanying play sound are so useful in the maintenance of a playful interaction.

Play signals (i.e., play faces, play vocalizations, and laughter) essentially function in all the same ways as social mammalian play (Gervais and Wilson 2005). They help foster physical, psychological, and social development while simultaneously spreading positive / affective emotions (Bachorowski and Owren 1999). Because laughing is the sending of a signal in the face of non-serious social incongruity, it would have been adaptive by inducing a positive state in others, thereby effectively recruiting them to engage and continue in social play. Thus, those individuals who were more adept at becoming playful during appropriate times, while also eliciting a playful state in others, would have found themselves with relatively increased individual and within-group fitness through the benefits of social play. These are functions that are similar to those served by play panting in chimpanzees (Matsusaka 2004) and those proposed for laughter in humans (Gervais et al. 2005; Weisfeld 1993).

Socially-stimulated laughter develops in human infants around four months of age, with tickle-induced laughter appearing about this time or shortly after. Laughter, smiling, and crying, whether evoked by tickling or other stimuli, are important means by which preverbal infants influence the behaviour of their mother and other caregivers (Plooij 1979). However, even after speech develops, tickling, laughter and other non-verbal signals remain important channels of communication with parents, family, and friends. In addition, like other laughter, that evoked by tickling virtually disappears in solitary individuals (Provine 1996, 2000). This is because tickling involves more than the sensory physiology of touch and the physical properties of the stimulus. It is a combination of vocal, facial, social, and emotional components, and is the product of a social interaction between a tickler, the person or thing administering the stimulus, and the ticklee, the person being stimulated. Tickle is more than simply a tactile reflex; it is a form of communication. Therefore, just as the relationship between individuals involved are key to comprehending tickling, tickling is essential to understanding the social vocalization with which tickling is associated (Provine 2000).

Imbedded in this theory is the argument that tickling is based on defense. It is argued that tickling responses developed under the influence of natural selection as a method of protection against attack and a warning of the approach of foreign bodies (Ellis 1927; Provine 2000; Weisfeld 1993, 1997). In other words, laughter induced by tickling is a substitute for the motor act of defense against injury (Roeckelein 2002) signaling the mock combat as a game and protecting against damage from misunderstandings. This hypothesis is supported by the fact that in humans and other animals, the most ticklish regions correspond to the most vulnerable areas of the body that are also the most vigorously defended in both real and play fighting (Ellis 1927; Provine 2000). The defensive movements of the tickle are complex, variable, goal-oriented, and more importantly, socially motivated. Tickle plays a central role in social engagement, locking the ticklee and the tickler into a give and take relationship that is at the base of all social play in both humans and nonhuman primates (Provine 1996).

In summary, the consensus among researchers (Matsusaka 2004; Matsuzwa 2001; Plooij 1979; Provine 1996, 2000; Van Hooff et al. 2003; Vettin et al. 2005) is that laughter may have began as a ritualization of the panting sound of rowdy play of which tickle was a trigger and central component. This has been exemplified by the laugh-like responses of chimpanzees which maintains its ancient pant-like properties and association with physical play. Today in humans, laughter has emancipated from this original context. Now, the heavy panting of play signals playful intent or anticipation even when the ongoing level of activity does not demand laboured breathing.

However, human laughter is one step removed from this pant-like vocalization and is elicited by a much wider range of stimuli, including conversation and humour. However, whether the “pant-pant” of chimpanzees or the abstract “ha-ha” of humans, the acoustic structure of laughter appears to have its roots in the respiratory sounds of physical play (Provine 1996). Thus, the analysis of facial expressions and non-verbal play vocalizations in other non-human primates beyond the chimpanzee in the context of tickling is significant when investigating possible precursors of human laughter.

1.4 Do non-human primates laugh?

Although some researchers still assert that laughter is a phenomenon confined to human beings (e.g., Apte 1985; Askenasy 1987; Hertzler 1970), further investigation with additional primate species is required to refute such a claim. In the past, too little was known about human laughter to permit rigorous comparison with other species, and even today there is very little documented research on the existence of laughter among primates. Not only is the body of ethological research on great ape laughter small, it consists of only a handful of studies with chimpanzees (e.g., Matsusaka 2004; Matsuzwa 2001; Plooij 1979; Provine et al. 2000; Van Hooff et al. 2003; Vettin et al. 2005) and one study with orangutans. Although limited, these studies suggest that laughter-like vocalizations do exist among chimpanzees in the context of tickling and play and support the possibility that laughter-like vocalizations similar to human laughter may exist in other animal species beyond humans. What follows is a brief outline of four of these chimpanzee studies followed by a more detailed section on the only other study undertaken with orangutans.

1.4.1 Chimpanzee laughter studies

The first of these studies was reported by Plooij in the late 1970s (Plooij, 1979). Plooij found that biting and play faces were first observed in chimpanzees around the third month of life. He reported that shortly after these behaviours appear, chimpanzee infants exhibit a behaviour that is similar, but should not be directly equated, to human laughter. This chimpanzee vocalization consists of staccato rhythmic breathing with escalating expellations of air. Plooij concluded that while not every occasion of tickling produces the laughter-like response, when they are produced, the vocalizations associated with smiling and tickling retain a central role in the social and communicative activity.

The second study was reported by Matsusaka (2004). In order to identify the social functions of human laughter and chimpanzee play panting, Matsusaka studied when chimpanzees exhibited play panting in social play and how these interactions were affected by the presence of vocalizations. He discovered that chimpanzees rarely emitted play panting to initiate a bout of social play, were more likely to play pant if a target of "aggressive" actions, and that infant chimpanzees were more likely to produce the vocalization if receiving "aggressive" actions from adolescent or mature individuals versus other infants or juveniles. As a result, the findings show that chimpanzee play panting serves as positive feedback for the play to continue. It prompts the play partner to keep providing playful stimulation in a situation that may contain the risk of excessive arousal and possible miscommunication of playful defense with real efforts to escape the situation (Matsusaka 2004).

In the third study, Vettin and Todt (2005) compared tickle-induced human laughter to the play vocalizations of chimpanzees and Barbary macaques. By examining some acoustic parameters, they discovered that chimpanzee play vocalizations occurred most often during play with close bodily contact (i.e., wrestling and tickling) and occurred in 50% of the encounters. Secondly, Vettin and Todt discovered that chimpanzee vocalizations are serially organized and that there is considerable intra-bout variability in interval durations and fundamental frequencies — two characteristic features of human laughter that, according to them, are crucial for deciding whether a given utterance will be identified as laughter. The third conclusion in this study was that chimpanzee vocalizations differed from human laughter in that the former were alternatively produced by expiration and inspiration. However, when only the expiratory elements were examined, human laughter did not actually differ from chimpanzee play vocalizations. Thus, Vettin and Todt's study shows that the play vocalizations in combination with the play face should be considered possible homologues of human laughter.

The fourth study hypothesized that in contrast with the human "ha-ha" laughter vocalization, chimpanzee play vocalizations can be characterized as guttural panting that lacks a voiced quality (Provine 2006). To test this hypothesis, Provine and Bard (see Provine 2000) compared the social and acoustic properties of tickle-evoked chimpanzee vocalizations with samples of human conversational laughter. Through spectrographic analysis, they measured the pitch and intensity of a vocalization over time and concluded that their hypothesis was correct. They also found that there was one important difference between the two species — that human laughter contains

several laugh pulses that occur during one expiration, whereas with chimpanzees, play vocalizations are produced during each brief expiration and inspiration.

1.4.2 Orangutan laughter study

While the evidence for the existence of laugh-like vocalizations among chimpanzees is reasonably well-established, so far there has only been one other attempt to determine whether laughter occurs in orangutans. The findings of this study were included in a PhD dissertation by Marina Davila Ross, titled *Towards the evolution of laughter: A comparative analysis on hominoids* (2007).

Ross conducted an extensive analysis of the vocalizations produced by various primate species when tickled. This included one siamang, five gorillas, four chimpanzees, five bonobos, seven orangutans, and three human infants. In addition, she examined the function of vocalizations during social play and the phenomenon of contagion among orangutans.

Ross reached three major conclusions. The first is that her research supported the Play-Activation Hypothesis originally named by Matsusaka (2004). This hypothesis states that the function of laughter among orangutans is not to appease aggression or fear but is rather a signal to maintain social play. Second, she concluded that the low-frequency vocalizations (also referred to as 'play panting' or 'staccato breathing' by other researchers) produced by great apes when tickled could be considered homologous to human laughter and thus aptly referred to as vocal laughter. This was based on the finding that all great apes in her study emitted these low-frequency vocalizations in this context despite differences in acoustic production, amplitude, and frequency as she went from *Pongo* to *Homo*.

Third, orangutans clearly were the species to laugh least during her tickling sessions, but when they did, they produced the most distinctive laughter among the great apes, predominantly producing squeaks. More specifically, Ross found that orangutan play vocalizations include both low frequency sounds, typically described as the panting, guttural staccato breathing mentioned above, in addition to high frequency tickling squeaks which were unique to the orangutans and a much more common response than the low frequency vocalizations. Furthermore, orangutan play vocalizations lack tonal structure which she states could be explained by differences in function or its effect on listeners. As a result, she states that not all non-human primate tickle-induced vocalizations can be considered homologous to humans. Rather, she infers that whereas the low-frequency vocalizations found in ancestral African apes

became a more effective acoustic signal and the predominant vocalization of play, among orangutans the high-frequency play "squeaks" assumed this role (Ross 2007, 2010).

1.5 Goals of this study

While there is a general consensus on the existence and characteristic features of great ape play faces, data on great ape play vocalizations and their relationship with play faces is scant. As previously discussed, very few studies have been published on laughter-like vocalizations accompanying play faces in great apes. However, it has been suggested from anecdotal reports on bonobos (de Waal 1998) and gorillas (Fossey 1972), in addition to the handful of studies on chimpanzees (see section 1.4.1; Ross 2007), and one on orangutans (Ross 2007), that the two responses are usually produced during rough and tumble social play and tickling.

Due to the fact that there is limited evidence for laughter in great apes and that this body of research does not extend much beyond chimpanzees, this study is a necessary and logical step in the search for laughter origins. By examining its existence among a species only recently explored, the following study will make an important contribution to this area of evolutionary research. In order to do so, this study tests four hypotheses:

1. Orangutans emit vocalizations when producing play faces. If so, it will indicate that orangutans have specific play face-play vocalization combinations that are potentially akin to human laughter.
2. There are sex differences in the presence and frequency of play faces and play vocalizations among orangutans in the context of tickling. If so, both play faces and play vocalizations will occur more frequently among male orangutans than among females.
3. There are age differences in the presence and frequency of play faces and play vocalizations among orangutans in the context of tickling. If so, the older orangutans will exhibit play faces and play vocalizations more frequently than the younger orangutans.
4. The length of time orangutan subjects have spent in rehabilitation will affect the presence and frequency of play faces and play vocalizations among orangutans when tickled. If so, play faces and play vocalizations will occur more frequently among those orangutans who have lived at the OQCC for a greater period of time due to socialization with humans and/or other orangutans.

In order to place this study in the larger framework, it is important to recognize that Ross' study (2007) was the first to offer support for the possibility that laughter-like vocalizations exist among orangutans. However, despite these important discoveries, her research failed to address several questions. As such, the goals of the current study differ in several ways as I address issues that have not yet been examined. The first issue pertains to context. Ross assessed the frequency and production of vocal laughter emitted during orangutan social play. From these observations, Ross determined that orangutans rely more heavily on facial expressions than vocalizations during play and found vocal laughter to only occur in 3.8% of the play bouts. However, in none of these play bouts was tickling among con-specifics observed. In contrast, I investigated the existence of play faces and vocalizations among orangutans, but in the context of tickling alone. By doing so, I attempt to uncover important information on the role and relationship of facial expressions and possible laughter vocalizations among orangutans in a context not yet directly researched.

The second difference involves the categorization of play faces and vocalizations. Ross' method of categorizing play faces combined the ROM and the OMBT into one category. In contrast, I looked at the four play faces independently of one another in addition to lumping them together as one phenomena. This decision was based on research undertaken by Van Hooff and Preuschoft (2003), who state that other than their theory that the ROM is ancestral to the OMBT, very little is known about the occurrence of these two facial displays in species other than the chimpanzees and bonobos. Palagi (2008) also states that the two may occur side by side within a species but they may also serve different functions. Thus, I felt it was sensible to examine all of the open-mouth play face variants — ROM, OMBT, open-mouth no teeth and the bite face, in relation to all vocalizations. Further to this point, Ross postulates that low-frequency vocalizations are homologous to human laughter. As a result, these types of vocalizations became the focus of her study. In the process, Ross concluded that orangutans mostly exhibit open-mouth faces (64%) (ROM and OMBT displays), non-relaxed faces (29%), and bite faces (8%) while emitting low-frequency vocalizations. In contrast, my study examined the composition of play face types co-occurring with all vocalization types in order to investigate the various vocal responses to tickling.

The third major difference between my study and that of Ross' is sample size. Ross recorded low-frequency vocalizations of five great ape species during tickling

sessions. By applying an acoustic and phylogenetic analysis, she tested the hypothesis that the low-frequency of great apes and humans were homologous. As mentioned above, her analysis supported that hypothesis. However, because she only utilized seven orangutans, I find it problematic to arrive at such a generalization of orangutan laughter vocalizations on the basis of seven individuals who were from two different facilities in two different countries (Malaysia and Germany). My research, on the other hand, is the first to study this behaviour using a much larger sample of infant individuals from the same location and under the same conditions. As a result, I feel the findings of this study will provide a more reliable base from which to draw conclusions on the existence of orangutan laughter.

The fourth difference between my study and Ross' is that I examined the socio-ecological effects of sex, age, and length of time in rehabilitation on orangutan facial and vocal displays evoked during tickling. The sex hypothesis was tested based on the fact that it has been suggested that primates that show a remarkable sexual dimorphism also have more pronounced sex differences in play behaviour (Stevenson & Poole 1982). In a paper on gorilla sex differences in play (Maestripieir and Ross 2004), it has been argued that given the sexual dimorphism in gorilla body size and the role assumed by the male in protecting the group from con-specifics and predators, the motor-training hypothesis of play predicts that male infants should exhibit higher frequencies of social play than female infants. The findings were consistent with this. Furthermore, of all the great apes, orangutans exhibit the most marked sexual dimorphism in body size and it has been observed by other researchers (e.g., Galdikas, personal conversation 2013, Maple 1980; Rijksen 1978) that there are distinct sex differences in orangutan play: males play more than females, females tend to withdraw from play, and social play duration of infant/juvenile males is double that of females. If male orangutans play more than females then we can assume that play vocalizations also play a critical role in these play / tickling sessions due to the importance for individuals to differentiate between real and play fighting. Thus, if we accept tickling as one aspect of social play and we support the motor-training hypothesis that male orangutans play more, it is likely that male infant orangutans will produce a higher frequency and a longer duration of both play faces and vocalizations during the context of tickling. As this has not yet been investigated, it would be an important contribution to the study of orangutan laughter.

The age hypothesis was tested based on the fact that young human children play and laugh more than babies or adults (Bainum, Lounsbury, & Pollio 1984; Martin & Kuiper 1999) and that young mammals, especially juveniles, play more than infants

or adults of the same species (Lewis 2005; Poirier, Bellisari & Haines, 1978). Thus, if play and laughter or laughter-like play vocalizations occur more in juvenile individuals, this study wanted to examine if the same could be said for orangutans. If so, the older orangutans in this study who were closer to juvenile age would play and vocalize more than the younger orangutans.

The time hypothesis was tested based on the fact that laughter is a social phenomenon. In fact, it has been noted that humans seldom laugh when alone. In contrast, orangutans are somewhat social but are more a semi-solitary species whose social circle mainly consists of non-receptive adult females with their young, with other adult females, and with adolescents who are not necessarily their own offspring. While the mother-young relationship is very intense and lasts for several years, the time spent with other orangutans is relatively short (Galdikas 2013). As a result of this social structure, orangutan play and the resulting play vocalizations would be limited to interactions with young individuals in their small social circle. In contrast, at the OQCC, infant orangutans are living and associating with several other infant and juvenile orangutans on a daily basis providing them with more opportunity for socializing and for play which would be more conducive to producing laughter-like vocalizations if they were to exist. Furthermore, at the OQCC, orangutans are in contact with and cared for by human caregivers who are present at a crucial time in their upbringing when they would normally be learning behaviours from their mothers if still in the wild. As such, if laughter exists among orangutans at this facility, perhaps this behaviour is one that is learned from their human counterparts. If so, it is likely that those individual orangutans who had spent more time in the OQCC would be more likely to produce play faces and vocalizations due to the socialization with humans and/or other orangutans of similar age.

The final difference between this and Ross' study is that mine solely studied the context of tickling. Tickling was chosen as the most appropriate research protocol because both it and social play are the main contexts in which laughter-like behaviour has been observed in chimpanzees. Due to the likelihood that this method would be one of the most reliable for producing a laugh-like response if one were to exist among orangutans, I, too, chose tickling as the stimulus for a number of reasons. First, it has been found to be the most reliable means for evoking similar responses in both chimpanzees and humans (Provine 1996, 2000; Vettin and Todt 2005). Second, when humans are tickled they often exhibit both laughter facial expressions and laughter vocalizations. Third, the laughter play face response found in humans resembles the ROM play face characteristically shown by some non-human primates during social

play of which tickling is one component. Fourth, tickling has frequently been observed during the social play of other great apes, particularly chimpanzees and bonobos, and it appears that they have the same ticklish regions of the body as humans (Provine 2000; van Lawick-Goodall 1971). Lastly, this method allowed me to quickly and reliably test a large number of individuals over a short period of time.

Chapter 2
Materials and Methods

This chapter is divided into three parts. The first outlines the methods used in the field to collect data. The second describes how the data were coded. The third part of the chapter describes the statistical analyses carried out to test the hypotheses.

2.1 Data Collection

The fieldwork was carried out between June 24 and July 6, 2007 at the Orangutan Care Centre and Quarantine (OCCQ) in Pasir Panjang in the province of Kalimantan Tengah, Indonesian Borneo.

Founded in 1998 by Dr. Birute Galdikas, the OCCQ was created for rescued ex-captive orangutans needing medical or other care in preparation for their eventual release back into the wild. At the time of the present study, there were approximately 300 orangutans at the OCCQ living in small wooden facilities (or pondoks) on the 80 hectares of primary peatswamp forest where many of the orangutans are released every day (Galdikas 2013).

The orangutans at the OCCQ live in one of seven pondoks that house individuals of different age and weight classes and in different phases of the rehabilitation process. The subjects used in this study were housed at three of these facilities—Pondok Cempedak, Pondok Waru and Pondok Penaga. The orangutans housed in Pondok Cempedak were between 1.5 and 3.5 years old and weighed between 3kg and 11 kg, while those housed in Pondok Waru were between 2 and 3.5 years old and weighed between 8.5kg and 12kg. The orangutans housed at Pondok Penaga were between 2 and 3.5 years old and weighed between 8.5kg and 14kg.

Data on Pondok Cempedak orangutans were collected behind their sleeping quarters at the play station where the infants spent their time eating, socializing and playing. Data on the Pondok Waru and Pondok Penaga orangutans were collected at two locations. To record data on rainy days or on Sundays, when the orangutans

remain at their respective housing facilities for bathing and pondok maintenance, the orangutans were taken outdoors to a small covered play platform adjacent to Pondok Waru. On other days, the Pondok Waru and Pondok Penaga orangutans were recorded on a feeding platform in the forest where the orphan orangutans learn locomotory, nest-building and foraging skills.

A total of 41 subjects were included in the study. Subjects were selected by a caregiver based on orangutan's availability, health, and desire to play, in addition to their proximity to caregivers and recording equipment. Table 2.1 provides details of the subjects used in the study, including their age, gender, weight, and date of admittance to the OCCQ. Twenty-four of the subjects were male and 17 were female. At the time of data collection, 11 of the subjects were between 13 and 24 months old, 20 were between 25 and 36 months old, and ten were between 37 and 48 months old. With regard to time spent in captivity, 21 subjects had been at the OCCQ a year or less, 16 had been there 13-24 months, and four had been there 25-42 months. There was also one orangutan (subject #5) who was estimated by the OCCQ veterinarians to be 24 months old yet she had been a resident at the Care Centre for 25.5 months. As a result, we placed this subject in the respective age and time groups according to the vets' approximations rather than tamper with the data provided.

Using tickling as a stimulus, a total of 152 tickle sessions were recorded. During these sessions, the orangutans were tickled on their palms, feet, armpits, neck, and abdomen by caregivers/assistants. The caregivers were asked not to speak or vocalize during the sessions in order to avoid recording disruption, and to minimize the chances of orangutans producing facial expressions or vocalizations for reasons other than in response to the tickling interaction.

Table 2.1: Orangutan Subject Data

Subject	Sex	Age in years	Age in months	Months at Care Centre
38. Maylene	F	1.5	18	3
18. Alexander	M	1.5	18	7
41. Erin	F	1.5	18	7
20. Gail	F	1.5	18	11
11. Hayes	M	1.5	18	17
12. Egol	M	1y10m	22	11
25. Emily	F	2	24	7
7. Dominic	M	2	24	13
15. Lodik	M	2	24	18
9. Lear	M	2	24	20
5. Glenda**	F	2	24	25.5
35. Jay	M	2.5	30	1.5
40. Mey Emily	F	2.5	30	1.5
17. Denox	F	2.5	30	4.5
19. Beatrix	F	2.5	30	6
3. Pascal	M	2.5	30	8
14. Donut	M	2.5	30	11
10. Morgan	M	2.5	30	15.5
13. Leslie	F	2.5	30	17
16. Monroe	F	2.5	30	20
8. Roberta	F	2.5	30	23
37. Runtu	M	2.5	30	4
24. Krista*	F	3	36	36
36. Bozes	M	3	36	3
26. Karbank	M	3	36	5
29. Irene	F	3	36	15.5
28. Nicole	F	3	36	17
32. Peter Aluy	M	3	36	17
4. Salosa	F	3	36	19
21. Sidney	M	3	36	24
31. Arapura	M	3	36	24
27. Ade	M	3.5	42	5
39. Hudi	M	3.5	42	5
6. Darren	M	3.5	42	11
1. Dr. Ann	F	3.5	42	12
34. Malcolm	M	3.5	42	13
33. Roy	M	3.5	42	25
2. Tim	M	3.5	42	41.5
30. Morison	M	4	48	1.5
22. Sinta	F	4	48	17.5
23. Omry	M	4	48	19

* Born at OCQQ **Age est. at 24 months but lived at OCCQ for 25.5 months

Recording started when the caregiver made physical contact with the orangutan and ended when the orangutan lost interest, failed to produce a response after several seconds, exhibited discomfort, or terminated the interaction by moving away. Recording was also terminated if the interaction was completely disrupted by weather, equipment difficulties, or another orangutan. Occasionally tickling or recording was interrupted but only very briefly. This occurred, for example, when the pause button was pressed accidently or the tickler was bitten. Because such disruptions were short and did not cause the tickling interaction to end (the orangutan continued to cooperate), I kept recording and referred to the entire tickling interaction as a session.

The tickle sessions were video-taped using either a Sony DCE-PC9 NTSC Video Camera or a Sony TRV 900 Video Camera. Sounds were recorded using a Sennheiser EW 122 G2 lapel microphone held above the orangutan's head by one of the field assistants.

2.2 Data Coding

Using a random number generator, one tickle session was selected for each orangutan. This was done for two reasons. First, because the number of tickle sessions for each orangutan varied from one to 11, a random sample allowed me to account for individuals who had been tickled more than once. Second, the random sample was also a way to avoid having to treat all samples of one individual as a single set as this would have added greatly to the time required for analysis.

Once the 41 tickle sessions had been chosen, facial expressions and vocalizations were identified, and their duration in seconds recorded. Facial expression identification for the play faces was based on the play faces or "laugh variants" discussed by Van Hooff and Preuschoft (2003). The authors recognize three play faces: 1) an open-mouth expression in which teeth are covered (OMNT); 2) relaxed open-mouth display where the lips are loose or slightly retracted, the mouth is moderately to widely open, and the lower row of teeth is bared but the upper row is covered (ROM); and 3) open-mouth bared-teeth display in which the lips are retracted, the mouth is widely open, and both rows of teeth are bared (OMBT). A fourth play face—the bite face—was added to the list based on its close resemblance to, and its inseparability from, the other play faces. The bite face was included in the play face category of this study based on prior research on chimpanzees and orangutans who have been witnessed to make a play face before they play bite (Matsusaka 2004, Ross

2007). Through personal observation, I also found the bite face to co-occur with other play face types during the tickling episodes. However, due to difficulty distinguishing between regular play faces, play bite faces, and actual biting, and determining where these expressions began or ended, as they often occurred in a sequence, I only recorded bite faces when they appeared with a vocalization. In terms of the non-play faces, their identification was based on personal observation and were generally divided into three main categories: 1) eek displays; 2) lips closed displays; and 3) other open-mouth variations that involved an open mouth of some sort but did not fall into any of the play face categories. The complete definitions for the facial expressions identified in this study can be found in Table 2.2.

Table 2.2: Characteristics of facial expressions identified in this study. OMNT, ROM and OMBT in accordance to van Hooff and Preuschoft (2003)

Display	Expression	Characteristics
PF 1	Open-Mouth No Teeth (OMNT)	Loose lips, Mouth moderately to widely open, No teeth bared
PF 2	Relaxed Open-Mouth (ROM)	Lips loose or slightly retracted, Lower row of teeth bared, Upper row of teeth covered, Mouth moderately to widely open
PF 3	Open-Mouth Bared Teeth (OMBT)	Lips retracted, Both rows of teeth bared Mouth wide open
PF 4	Bite face	Starts out as one of the above, Attempt to bite is apparent
Non-play face	Eek Face	Lips long and tight, One or both rows of teeth exposed Mouth makes the shape as a human would if saying the word “eek” in an exaggerated manner
	Lips Closed	No teeth exposed Face could be relaxed or non-relaxed, didn’t differentiate
	Other Open-Mouth Variations	Involves an open mouth of some sort with variations on the number of rows of teeth exposed Other characteristics seen in these faces include the following in different combinations: tongue out, underbite, lips long and tight, clenched teeth, hand covering mouth, biting lip, protruding lips, or curled lips

I analyzed the videos twice. First, I identified and timed the instances in which a vocalization was produced, and recorded the associated facial expression. The second time, I identified and timed the instances in which a facial expression was produced and recorded any associated vocalization.

2.3 Testing of hypotheses

Once the initial identification was finished, a number of calculations were carried out. First, I tallied the total number of entries in each subject's session where vocalizations were produced with any type of facial expression. I also computed the number of entries in each session where play faces co-occurred with any type of vocalization.

The above data were then summarized in tables. This was done for three different groups of data: sex, age, and length of time in rehabilitation. Each of the hypotheses addressing the three social-ecological factors were then examined according to three sets of data: the presence of play face versus non-play face, the frequency of the four different types of play faces, and the presence of vocalized versus silent play faces.

In order to calculate the results, one or two types of analyses were conducted: Chi-Squared was employed for all four hypotheses in this study to assess the overall presence and frequency of laughter. In addition, Spearman's Coefficient Correlation was conducted using the variables of age and time to analyze the strength of these factors in their relationship with the presence and frequency of laughter.

2.3.1 Hypothesis #1: Orangutans emit play vocalizations when tickled

Do Orangutans respond to tickling with play faces?

This analysis investigated whether the number of play faces exceeded the number of non-play faces.

First, the Chi-Squared test was applied to determine whether each individual's number of play faces exceeded the number of play faces to be expected if the subject was simply responding to the tickling with a play face or non-play face at random. There were two potential outcomes — play face or non-play face. So, the expected frequency was 50% of the number of responses given by each individual. This part of the analysis tells us whether some individuals exhibited play faces more frequently than would be expected on the basis of chance alone.

Subsequently, the Chi-squared test was used to determine whether the number of individuals who displayed a significant frequency of play face response in the first analysis exceeded what one would expect on the basis of chance alone. In the first part of the analysis, individuals could either return a significant frequency of play face response or not. As such, the expected frequency of significant play face response in

the second part of the analysis was 1/3 of the number of individuals who produced a significant frequency of play face response in the first part of the analysis. The remaining 2/3 consisted of the number of individuals who produced other outcomes: either a significant frequency of non-play face response or a completely random response. This part of the analysis indicated whether there was a sample-level tendency for orangutans to respond to tickling with a play face.

Throughout this section, where applicable, Yates correction was applied (Shennan 1997). This meant that if any cell in a table had an expected value (E) of five or less, I subtracted 0.5 from every positive (observed minus expected) value or added 0.5 to every negative (observed minus expected) value before squaring it and dividing it by the expected value. This was also the case in the other sections that follow where Chi-squared analysis was used.

Do orangutans have a preference for particular play faces?

This analysis investigated whether the frequencies of the four types of play face differed significantly. It included only those individuals that responded with a play face. Non-play face responses were ignored in the analysis.

First, the Chi-Squared test was used to assess whether the observed number of each of the four play face types for each individual exceeded the number of play faces to be expected if the subject was simply responding to the tickling with one of the four play faces at random. There were four potential outcomes, so the expected frequency for each play face type was 25% of the total number of play faces for each individual. This part of the analysis identified individuals whose play face frequencies departed significantly from random (i.e., individuals who have a preference for a certain play face over others).

Subsequently, the Chi-squared test was used to determine whether the number of individuals who displayed a significant frequency for a particular play face response in the first analysis exceeds what one would expect on the basis of chance alone. In the first part of the analysis, individuals could return a significant frequency for particular play face types or not. As such, the expected frequency of individuals with a significant departure in the second part of the analysis was 1/5 the number of individuals who produced a significant play face type response in the first part of the analysis. The remaining 4/5 consisted of the number of individuals who produced other outcomes: significant frequency of one of the other three play face types or a completely random response. This part of the analysis indicated whether there was a

sample-level tendency for orangutans to respond to tickling with a particular play face type.

Are play faces accompanied by vocalizations?

This analysis investigated whether the play faces specifically were accompanied by vocalizations. Only those individuals that responded with a play face were included.

First, the Chi-squared test was used to assess the departure from chance of the frequencies of vocalized and silent play faces for each individual. There were two potential outcomes (vocalized play face or silent play face), so the expected frequency for vocalized play faces was 50% of the total number of play face responses for each individual. This part of the analysis identified individuals who exhibited vocal play faces significantly more often than was expected on the basis of chance alone.

Subsequently, the Chi-squared test was used to determine whether the number of individuals who displayed a significant frequency of vocalized play face response in the first analysis exceeded what we would expect on the basis of chance alone. As indicated in the first part of the analysis, individuals could either return a significant frequency of vocalized play face response or not. As such, the expected frequency for the second part of the analysis was calculated in the same way as described in section 2.3.1.1 to determine whether there was a sample-level tendency for orangutans to respond to tickling with a vocalized play face.

2.3.2 Hypothesis #2: There are sex differences in the occurrence of laughter in *Pongo*

Do male and female orangutans differ in the frequency with which they respond with play faces and non-play faces?

This analysis investigated how male and female orangutans differ in the frequency with which they respond with play faces and non-play faces. The results from the Chi-squared analysis described in section 2.3.1.1 were also used in this section. However, the individuals who exhibited a significant frequency of play face response were then tallied according to sex. Thereafter, the number of males who displayed a significant frequency of play face response was compared to the number of females who displayed a significant frequency of play face response.

In this section, we wanted to know whether the difference between the proportion of males who displayed a significant frequency of play face response and the proportion of females who displayed a significant frequency of play face response was significant or not. In this analysis, we used the Chi-squared test again. In the first part of the analysis, males and females could either return a significant frequency of play face response or not. Because the sample had a different number of individuals within each sex group, the expected frequencies in the second part of the analysis were calculated as follows. For the males, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of play face response in the first part of the analysis multiplied by the portion of the sample that were male (13/21). For the females, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of play face response in the first part of the analysis multiplied by the portion of the sample that were female (8/21). Thus, if males and females responded to tickling in the same way, 62% of the total number of individuals who displayed a significant frequency of play face response should be male and 38% should be female.

Are there sex differences in play face preference?

This analysis investigated whether male and female orangutans differ in the frequencies of the four types of play face and included only those individuals that responded with a play face.

The results from the Chi-squared analysis described in section 2.3.1.2 were also used in this section. Subsequently, the number of individuals who exhibited a significant frequency of a specific play face response was tallied within each sex group. Thereafter, the number of males whose play face frequencies departed significantly from random was compared to the number of females whose play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of males whose play face frequencies depart significantly from random and the proportion of females whose play face frequencies depart significantly from random was significant or not.

To determine which play faces were preferentially displayed by each sex, the play face tallies for the individuals whose play face frequencies depart significantly from random were compared. Were there any patterns in the play face frequencies?

For example, did all the males or all the females exhibit a preference for the same place face? If so, the play face with the highest number of significant frequencies was used for further analysis at the sample level.

In the second part of the analysis, we used the Chi-squared test again. The expected frequencies were calculated using the methods outlined in section 2.3.2.1 but using the data for the play face type which had the highest number of significant frequencies for both males and females. This was done in order to determine whether males and females preferentially display the same or different play faces in response to tickling.

Are there sex differences in the frequency of vocalized play faces versus silent play faces?

This analysis investigated whether males and females differ in the frequency with which they respond with silent play faces versus vocalized play faces. As in the previous analyses, only those individuals that responded with a play face were included.

First, the Chi-squared test was used as per the methods outlined in section 2.3.1.3. Subsequently, the number of individuals who exhibited a significant frequency of either a silent or vocalized play face response was tallied within each sex group. Thereafter, the number of males whose silent or vocalized play face frequencies departed significantly from random was compared to the number of females whose silent or vocalized play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of males who exhibit vocal or silent play faces significantly from random and the proportion of females who exhibit vocal or silent play faces significantly from random was significant or not. Were there any patterns in these play face type responses. For example, did all the males or all the females exhibit a preference for either vocal or silent play faces?

In the second part of the analysis, we used the Chi-squared test again to assess both the silent and vocalized play face responses. The expected frequencies were calculated as per the methods outlined in section 2.3.2.1. This analysis was done in order to determine whether males and females preferentially displayed a silent or vocalized play face in response to tickling.

2.3.3 Hypothesis #3: There are age differences in the occurrence of laughter in *Pongo*

Does the age of an orangutan affect the frequency with which they respond with play faces and non-play faces?

This analysis investigates whether infant orangutans of different ages differ in the frequency with which they respond with play faces and non-play faces.

The results from the Chi-squared analysis described in section 2.3.1.1 were also used in this section. However, the individuals who exhibited a significant frequency of play face response were then tallied within each age group. Thereafter, the number of individuals in age group 1 who displayed a significant frequency of play face response was compared to age group 2 and 3.

In this section we wanted to know whether the difference between the proportion of individuals in each age group who displayed a significant frequency of play face response was significant or not. In the second part of the analysis we used the Chi-squared test again. In the first part of the analysis, orangutans in three age groups could either return a significant frequency of play face response or not. Because the sample had a different number of individuals within each age group, the expected frequencies in the second part of the analysis were calculated as follows. For age group 1, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 1 (7/21). For age group 2, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 2 (8/21). For age group 3, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 3 (6/21). Thus, if individuals of various ages responded to tickling in the same way, 33% of the total number of individuals who displayed a significant frequency of a play face response should be in age group 1, 38% should be in age group 2, and 29% should be in age group 3.

As an additional analysis, the Spearman's Correlation test was also used. This involved the production of two-tailed, bivariate scatterplot graphs and non-parametric correlations using both raw and percentage data. As correlation coefficients are always

between -1 and +1, the following guidelines were followed when interpreting the r values: -1 to -0.7 (strong negative association), -.07 to -0.3 (weak negative association), -0.3 to +0.3 (little to no association), +0.3 to +0.7 (weak positive association), and +0.7 to +1.0 (strong positive association) (Ratner, B. http://www.dmstat1.com/res/ TheCorrelationCoefficientDefined.html Accessed January 16, 2013).

Are there age differences in play face preference?

This analysis investigated whether orangutans of different ages differed in the frequencies of the four types of play face and included only those individuals that responded with a play face.

The results from the Chi-squared analysis described in the first part of section 2.3.1.2 was also used in this section. Subsequently, the number of individuals who exhibited a significant frequency of a significant play face response was tallied within each age group. Thereafter, the number of individuals in age group 1 whose play face frequencies departed significantly from random was compared to the number of individuals in groups 2 and 3 whose play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of individuals in each age group whose play face frequencies depart significantly from random was significant or not.

To determine which play faces were preferentially displayed by each age group, the play face tallies for the individuals whose play face frequencies departed significantly from random were compared. Were there any patterns in the play face frequencies? For example, did all the subjects in age groups 1, 2 and 3 exhibit a preference for the same play face? If so, the play face with the highest number of significant frequencies was used for further analysis at the sample level.

In the second part of the analysis, we used the Chi-squared test again. The expected frequencies were calculated using the methods already outlined in section 2.3.3.1. This was done to determine whether infant orangutans within different age group preferentially displayed the same or different play faces in response to tickling.

As an additional analysis, the Spearman's Correlation test was also used as previously outlined in section 2.3.3.1.

Are there age differences in the frequency of vocalized play faces versus silent play faces?

This analysis investigated whether infant orangutans of different ages differ in the frequency with which they respond with silent play faces versus vocalized play faces. As in the previous analyses, only those individuals that responded with a play face are included.

First, the Chi-squared test was used as per the methods outlined in section 2.3.1.3. Subsequently, the number of individuals who exhibited a significant frequency of either a silent of vocalized play face response was tallied within each age group. Thereafter, the number of individuals in age group 1 whose silent or vocalized play face frequencies departed significantly from random was compared to the number of individuals in groups 2 and 3 whose silent or vocalized play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of individuals in each age group whose silent or vocal play face frequencies depart significantly from random was significant or not. Were there any patterns in these play face type responses? For example, did all the orangutans in each age group exhibit a preference for either silent of vocalized play faces?

In the second part of the analysis, we used the Chi-squared test again. The expected frequencies were calculated using the methods already outlined in section 2.3.3.1. This was done to determine whether infant orangutans within different age group preferentially displayed silent or vocalized play faces in response to tickling.

As an additional analysis, the Spearman's Correlation test was also used as previously outlined in section 2.3.3.1.

2.3.4 Hypothesis #4: Time in rehabilitation affects the occurrence of laughter in *Pongo*

Does the amount of time an orangutan spends in rehabilitation affect the frequency with which they respond with play faces and non-play faces?

This analysis investigated whether time spent in rehabilitation affected the frequency with which an infant orangutan responded with play faces and non-play faces. The results from the Chi-squared analysis described in section 2.3.1.1 were also used in this section. However, the number of individuals who exhibited a significant frequency of play face response was tallied within each time group.

The results from the Chi-squared analysis described in section 2.3.1.1 were also used in this section. However, the individuals who exhibited a significant frequency of play face response were then tallied within each time group. Thereafter, the number of individuals in time group 1 who displayed a significant frequency of play face response was compared to time groups 2 and 3.

In this section we wanted to know whether the difference between the proportion of individuals in each time group who displayed a significant frequency of play face response was significant or not. In the second part of the analysis we used the Chi-squared test again. In the first part of the analysis, orangutans in the three time groups could either return a significant frequency of play face response or not. Because the sample had a different number of individuals within each time group, the expected frequencies in the second part of the analysis were calculated as follows. For time group 1, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 1 (6/21). For time group 2, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 2 (12/21). For time group 3, the expected frequency in the second part of the analysis was the total number of individuals who produced a significant frequency of a play face response in the first part of the analysis multiplied by the portion of the entire sample that were in group 3 (3/21). Thus, if individuals who have spent different amounts of time in rehabilitation were responding in the same way, 29% of the total number of individuals who displayd a significant frequency of a play face response should be in time group 1, 57% should be in time group 2, and 14% should be in time group 3.

Where applicable, Yates correction was applied. As an additional analysis, the Spearman's Correlation test is also used as previously outlined in section 2.3.3.1.

Does time in rehabilitation affect play face preference?

This analysis investigated whether time spent in rehabilitation affected the frequencies of the four types of play face. It included only those individuals that responded with a play face.

The results from the Chi-squared analysis described in the first part of section 2.3.1.2 was also used in this section. Subsequently, the number of individuals who

exhibited a significant frequency of a particular play face response was tallied within each time group. Thereafter, the number of individuals in time group 1 whose play face frequencies departed significantly from random was compared to the number of individuals in time groups 2 and 3 whose play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of individuals in each time group whose play face frequencies depart significantly from random was significant or not.

To determine which play faces were preferentially displayed by each time group, the play face tallies for the individuals whose play face frequencies departed significantly from random were compared. Were there any patterns in the play face frequencies? For example, did all the subjects in time groups 1, 2 and 3 exhibit a preference for the same play face? If so, the play face with the highest number of significant frequencies was used for further analysis at the sample level.

In the second part of the analysis, we used the Chi-squared test again. The expected frequencies were calculated using the methods already outlined in section 2.3.4.1. This was done to determine whether individuals who had spent different amounts of time in rehabilitation preferentially displayed the same or different play faces in response to tickling.

As an additional analysis, the Spearman's Correlation test was also used as previously outlined in section 2.3.3.1.

Time in rehabilitation affects the frequency of vocalized play faces versus silent play faces?

This analysis investigated whether time spent in rehabilitation affected the frequency with which an infant orangutan responded with silent play faces versus vocalized play faces. As in the previous analyses, only those individuals that responded with a play face were included.

First, the Chi-squared test was used as per the methods outlined in section 2.3.1.3. Subsequently, the number of individuals who exhibited a significant frequency of either a silent of vocalized play face response was tallied within each time group. Thereafter, the number of individuals in time group 1 whose silent or vocalized play face frequencies departed significantly from random was compared to the number of individuals in time groups 2 and 3 whose silent or vocalized play face frequencies departed significantly from random.

In this section, we wanted to know whether the difference between the proportion of individuals in each time group whose silent or vocal play face frequencies depart significantly from random was significant or not. Were there any patterns in these play face type responses? For example, did all the orangutans in each time group exhibit a preference for either silent of vocalized play faces?

In the second part of the analysis, we used the Chi-squared test again. The expected frequencies were calculated using the methods already outlined in section 2.3.4.1. This was done to determine whether orangutans who had spent different lengths of time in rehabilitation preferentially displayed silent or vocalized play faces in response to tickling.

As an additional analysis, the Spearman's Correlation test was also used as previously outlined in section 2.3.3.1.

Chapter 3
Results

3.1 Hypothesis 1 (all subjects)

In this section of the study, I tested the hypothesis that play faces and vocalizations co-occur among orangutans in my sample more frequently than we would expect on the basis of chance alone. To do so, I examined the presence and frequency of play faces and vocalizations among orangutans when tickled. The full sample (N=21), regardless of age, sex, or time in rehabilitation, was considered.

In terms of the full sample size, it is important to note that of the 41 individual subjects used in this study, 27 orangutans responded in the tickling episodes in some capacity. Two of these individuals produced vocalizations but their facial expressions could not be recorded (N=25). They were excluded from the calculations. In addition, there were four individuals who responded five times or less. Due to analytical constraints, it was advised that they, too, be excluded from the calculations. Thus, for calculation purposes, the full sample was 21. It included those orangutans who produced a facial expression of any kind (whether accompanied by a vocalization or not) which could be successfully recorded.

3.1.1 Number of occurrences

Presence of play face versus non-play face

The results for the presence of play faces versus non-play faces for all subjects are summarized in Table 3.1.

When the entire sample was examined, play faces occurred 70% of the time, were over two times more common than the non-play faces, and were observed between 7–88 times. The non-play faces were produced 30% of the time and ranged between 0–100 times.

Table 3.1: Play face versus non-play face — full sample

Subject	PF	No PF	Total
2. Tim	19	28	47
3. Pascal	78	3	81
6. Darren	20	1	21
7. Dominic	46	28	74
9. Lear	55	74	129
10. Morgan	88	4	92
11. Hayes	9	19	28
12. Egol	33	1	34
15. Lodik	63	1	64
21. Sidney	15	4	19
23. Omry	41	0	41
27. Ade	14	0	14
33. Roy	7	2	9
1. Dr. Ann	8	2	10
4. Salosa	64	2	66
5. Glenda	15	3	18
8. Roberta	78	100	178
13. Leslie	13	23	36
16. Monroe	52	27	79
29. Irene	49	3	52
41. Erin	20	10	30
Total	787	335	1122

There was also considerable inter-individual variation in the frequency of play faces. Some individuals had relatively similar numbers for both types of expressions while others responded with a play face in every tickle episode.

In order to test this, chi-squared analysis was used. There were 13 out of 21 cases in which a play face occurred more often than a non-play face. This difference was statistically significant. When the play face frequency was compared to all other outcomes, the χ^2 value for the 21 individuals was 7.71. The minimum significant χ^2 values for p=0.01 at one degree of freedom was 6.64. As such, a play face response occurred much more frequently than was expected on the basis of chance alone. Hypothesis was supported: Play faces occurred more often than non-play faces.

Frequency of different play face types

The results for the presence and frequency of the four play face types for all subjects are summarized in Table 3.2.

Table 3.2: Play face types — full sample

Subject	PF 1	PF 2	PF 3	PF 4	Total
2. Tim	0	6	13	0	19
3. Pascal	0	8	47	23	78
6. Darren	0	3	16	1	20
7. Dominic	0	2	34	10	46
9. Lear	0	0	36	19	55
10. Morgan	1	19	67	1	88
11. Hayes	1	3	3	2	9
12. Egol	0	0	32	1	33
15. Lodik	0	0	19	44	63
21. Sidney	0	1	12	2	15
23. Omry	0	0	40	1	41
27. Ade	0	0	13	1	14
33. Roy	0	0	6	1	7
1. Dr. Ann	1	1	5	1	8
4. Salosa	1	5	53	5	64
5. Glenda	1	0	11	3	15
8. Roberta	1	1	70	6	78
13. Leslie	1	0	10	2	13
16. Monroe	0	2	49	1	52
29. Irene	2	0	47	0	49
41. Erin	0	0	20	0	20
Total	9	51	603	124	787

PF 1, the open-mouth no teeth display, was exhibited by the least number of subjects and occurred the least number of times, making up 1.14% (9/787) of the total play faces. Some subjects displayed this face once or twice but most did not display it at all.

PF 2, the relaxed open-mouth display, was also displayed infrequently, making up only 6.5% (51/787) of the total play faces. Although one individual responded 19 times, half of the subjects responded between one and eight times while the other half did not respond with this expression at all.

PF 3 was displayed by all subjects and occurred much more frequently than the other play faces, making up 76.6% (603/787) of the total play faces. While only five

individuals displayed this face under six times, six individuals displayed this facial expression up to 20 times, and over half of the subjects were found to reveal this expression between 20 and 70 times.

PF 4, the bite face, was the second most popular play face as it was exhibited by all but three individuals and made up 15.8% (124/787) of the total play faces. Four individuals displayed this expression between 10 and 44 times, while the remaining majority of the subjects responded only once or twice.

There were 18 cases out of 21 in which a PF 3 occurred more often than a PF 1, PF 2, or PF 4. As a result, the frequency of the PF 3 was compared to all other outcomes. The difference was statistically significant. The χ^2 value for this play face response for the 21 individuals was 52.65. The minimum significant χ^2 value for p=0.001 at one degree of freedom was 10.83. As such, the PF 3 response occurred significantly more frequently than was expected on the basis of chance alone. From this, it can be concluded that when orangutans produce a play face, they exhibit a preference for an open-mouth bared teeth display.

Silent versus vocal play faces

This section looked more specifically at the number of play faces that were produced with a vocalization. It was found that there was considerable inter-individual variation in terms of whether or not a play face was accompanied by a vocalization in response to tickling. The results for the presence of vocalized versus silent play faces are presented in Table 3.3 wherein the four play face types are combined. While two individuals produced only silent play faces, 19 out of 21 subjects produced both silent and vocal play faces. These ranged from 3–76 and 0–47, respectively. It was also revealed that while only one individual had equal numbers of both (23), 76% (16/21) of the subjects produced a higher number of silent play faces. Overall, silent play faces were much more common than the vocalized, making up 75% (588/787) of the total play faces and being nearly three times higher than the vocalized play faces. Therefore, while some orangutans emitted vocalizations while exhibiting play faces, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study.

Table 3.3: Silent versus vocal play faces — full sample

Subject	Silent play face	Vocal play face	Total
2. Tim	12	7	19
3. Pascal	76	2	78
6. Darren	20	0	20
7. Dominic	23	23	46
9. Lear	47	8	55
10. Morgan	41	47	88
11. Hayes	4	5	9
12. Egol	24	9	33
15. Lodik	59	4	63
21. Sidney	9	6	15
23. Omry	38	3	41
27. Ade	14	0	14
33. Roy	3	4	7
1. Dr. Ann	6	2	8
4. Salosa	60	4	64
5. Glenda	13	2	15
8. Roberta	43	35	78
13. Leslie	9	4	13
16. Monroe	49	3	52
29. Irene	24	25	49
41. Erin	14	6	20
Total	588	199	787

To test the above, the intention was to use Chi-squared analysis. However, these calculations were not necessary because there were no cases in which vocalized play faces occurred significantly more frequently than silent play faces. As such, the hypothesis was not supported. Some orangutans emitted vocalizations while exhibiting play faces, but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study.

3.2 Hypothesis 2 (sex effects)

In this section of the study, I tested the hypothesis that sex affects the presence and frequency of play faces and vocalizations in orangutans. All 21 subjects were divided into two groups based on sex: males (N=13), females (N=8).

3.2.2 Number of occurrences

Presence of play face versus non-play face

The results for the presence of play faces versus non-play faces for the two sex groups are summarized in Table 3.4.

Table 3.4: Play face versus non-play face — sex

Subject	PF	No PF	Total
Males			
2. Tim	19	28	47
3. Pascal	78	3	81
6. Darren	20	1	21
7. Dominic	46	28	74
9. Lear	55	74	129
10. Morgan	88	4	92
11. Hayes	9	19	28
12. Egol	33	1	34
15. Lodik	63	1	64
21. Sidney	15	4	19
23. Omry	41	0	41
27. Ade	14	0	14
33. Roy	7	2	9
Total	488	165	653
Females			
1. Dr. Ann	8	2	10
4. Salosa	64	2	66
5. Glenda	15	3	18
8. Roberta	78	100	178
13. Leslie	13	23	36
16. Monroe	52	27	79
29. Irene	49	3	52
41. Erin	20	10	30
Total	299	170	469
Grand Total	787	335	1122

Sub-dividing the sample by sex did not alter the finding that play faces were more common than non-play faces in both groups (males: 488 vs 165; females: 299 vs 170). Sub-dividing the sample by sex also did not affect the finding that there was considerable inter-individual variation in whether or not an orangutan exhibited a play face in response to tickling. Among the males, 11 of the 13 subjects produced both types of facial expressions but they were three times more likely to display a play face than a non-play face (488 vs 165). Only three individuals produced a higher number of

non-play faces than play faces and while these ranged from 0–74, nine of these male subjects exhibited a non-play face less than five times. On the other hand, the play faces were more evenly distributed with a range of 7–88 with only two individuals exhibiting a play face less than ten times. For the female group, all eight subjects produced both types of facial expressions, although the play faces were two times more common than the non-play faces. The range for the latter was between two and 100 although five of these were ten times or less with one individual skewing the results with 100 occurrences. The play faces ranged from 8–78 and they were more evenly distributed although the majority (n=5) had numbers over 20.

Turning now to the differences between the sexes, the males produced 653 of the 1122 (58%) total tickle responses. Of these, 75% (488/653) consisted of play faces while 25% (165/653) were non-play faces. The females produced 469 of the 1122 (42%) total tickle responses. Of these, 64% (299/469) were play faces whereas 36% (170/469) were non-play faces.

In this section where I was testing whether sex affected the presence of play faces among orangutans, it was found that overall play faces were more common than non-play faces. This was more so for the males who produced play faces one and a half times more frequently than the females (488 vs 299). Using this data, there appears to be some evidence that sex may affect response to tickling such that males are more likely than females to respond with a play face. However, if one compares the average number of play face responses between the males and females, they were equal at 37.5 and 37.4, respectively.

To test the above, the chi-squared test was used. The χ^2 value for the play face response for both sexes was .07. The minimum significant χ^2 value for p=.05 at one degree of freedom was 3.84. As such, the hypothesis was not supported: Neither sex exhibited a play face significantly more than the other.

Play face types

The results for the presence and frequency of the four play face types for males and females are summarized in Table 3.5.

Table 3.5: Play face types — sex

Subject	PF 1	PF 2	PF 3	PF 4	Total
Males					
2. Tim	0	6	13	0	19
3. Pascal	0	8	47	23	78
6. Darren	0	3	16	1	20
7. Dominic	0	2	34	10	46
9. Lear	0	0	36	19	55
10. Morgan	1	19	67	1	88
11. Hayes	1	3	3	2	9
12. Egol	0	0	32	1	33
15. Lodik	0	0	19	44	63
21. Sidney	0	1	12	2	15
23. Omry	0	0	40	1	41
27. Ade	0	0	13	1	14
33. Roy	0	0	6	1	7
Total	2	42	338	106	488
Females					
1. Dr. Ann	1	1	5	1	8
4. Salosa	1	5	53	5	64
5. Glenda	1	0	11	3	15
8. Roberta	1	1	70	6	78
13. Leslie	1	0	10	2	13
16. Monroe	0	2	49	1	52
29. Irene	2	0	47	0	49
41. Erin	0	0	20	0	20
Total	7	9	265	18	299
Grand Total	9	51	603	124	787

Sub-dividing the sample by sex did not alter the finding that PF 3 was much more common than the other play faces. In fact, PF 3 made up 77% (603/787) of the total play faces, 69% (338/488) of the total play faces for males, and 89% (265/299) of the total play faces for females. PF 3 was exhibited by all individuals in both categories and was much higher in occurrences than the other play faces.

At 338 occurrences, the male PF 3 was three times higher than the PF 4 at 106, followed by PF 2 at 42 and PF 1 at only two occurrences. For the females, while the order was similar, the number of occurrences was slightly lower for PF 3 at 265. PF 4, PF 2, and PF 1 followed distantly at 18, 9, and 7 times, respectively.

Sub-dividing the sample by sex also did not affect the finding that there was considerable inter-individual variation in terms of the play face types exhibited by orangutans in response to tickling. For the males, PF 1 was produced once by two individuals. PF 2 ranged from 0-19, PF 3 from 3-67 and PF 4 from 0-44. Only two

males exhibited all four displays. For the females, PF 1 ranged from 0-2, PF 2 from 0-5, PF 3 from 5-70, and PF 4 from 0-6. Three females exhibited all four play faces. According to this data, there appeared to be no particular pattern in predicting preference for a particular play face.

Turning now to the difference between sexes, the males had the highest number of all play faces except PF 1 where the females displayed this face seven times to the males' two. However, for the other play faces, the males had much higher numbers than the females: PF 2: 42 vs 9; PF 3: 338 vs 265; PF 4: 106 vs 18. In terms of the PF 3 which was the most common expression, among the males, the PF 3 was observed 338 times, making up 56% (338/603) of the total PF 3. For the females, PF 3 was seen 265 times, making up 44% (265/603) of the total PF 3.

To test the above, chi-squared analysis was used. The χ^2 value for the PF 3 response for both sexes was 0.005. The minimum significant χ^2 value for p=.05 at one degree of freedom was 3.84. As such, neither sex group exhibits a PF 3 significantly more than the other. The hypothesis was not supported: There are no sex differences in play face preference.

Silent versus vocal play faces

This section looked specifically at the number of play faces that were produced with a vocalization. It was found that sub-dividing the sample by sex did not affect the finding that there was considerable inter-individual variation in terms of whether or not play faces were accompanied by a vocalization in response to tickling. The results for the presence of vocalized versus silent play face responses are presented in Table 3.6 wherein the four play faces are combined. With the males, 11/13 individuals produced both the silent and vocalized play faces which ranged from 3–76 and 0–47, respectively. While three male subjects had a higher number of vocalized play faces and one had an equal number of both, the majority of individuals revealed a greater likelihood of producing a silent play face. In the female group, all eight subjects produced both the silent and vocal play faces which ranged from 5–60 and 2–35, respectively. Only one individual had a greater number of vocalized play faces over the silent by a small margin (25 vs 24). Therefore, it was also more likely for the females to produce a silent play face than a vocalized one. Overall, for both sex groups, not only were the silent play faces more common than the vocalized, the ranges were more evenly distributed and the occurrences were much higher in number.

Table 3.6: Silent versus vocalized play face — sex

Subject	Silent PF	Vocal PF	Total
Males			
2. Tim	12	7	19
3. Pascal	76	2	78
6. Darren	20	0	20
7. Dominic	23	23	46
9. Lear	47	8	55
10. Morgan	41	47	88
11. Hayes	4	5	9
12. Egol	24	9	33
15. Lodik	60	4	64
21. Sidney	9	6	15
23. Omry	38	3	41
27. Ade	14	0	14
33. Roy	3	4	7
Total	371	118	489
Females			
1. Dr. Ann	5	2	7
4. Salosa	60	4	64
5. Glenda	13	2	15
8. Roberta	43	35	78
13. Leslie	9	4	13
16. Monroe	49	3	52
29. Irene	24	25	49
41. Erin	14	6	20
Total	217	81	298
Grand Total	588	199	787

Turning now to the differences between the sexes, the males produced the most vocal play faces at 59% (118/199) out of the total number of vocal play faces for both groups. The silent play faces made up 76% (371/489) out of the total play faces for this group which was three times higher than the vocalized play faces. Conversely, the females produced 41% (81/199) of the total number of vocalized play faces for both sex groups. Silent play faces made up 73% (217/298) of the total play faces for this group which was also nearly three times higher than the vocalized play faces.

Overall, silent play faces were much more common than the vocalized, making up between 73 and 76% of the total play faces for each group and being three times higher than the vocalized play faces. While the males had higher numbers of both play faces types, both sexes produced a much higher number of silent play faces than vocalized. Overall, the males made up 63% (371/588) of the total silent play faces for

both sex groups, 59% (118/199) of the total vocal play faces for both sex groups, and 62% (489/787) of all play faces (both silent and vocal) for both sex groups.

My intention was to use the chi-squared analysis to test the above with both the silent and vocalized play face responses. However, calculations were not necessary for the latter as there were no cases in which a vocalized play face occurred significantly more frequently than a silent play face for either group. For the silent play face, the χ^2 value for this response was 0.04. The minimum significant χ^2 value for p=.05 at one degree of freedom was 3.84. As such, the hypothesis was not supported. Some orangutans emitted vocalizations while exhibiting play faces, but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. In addition, there were no significant sex differences in the number of silent play faces displayed when orangutans were tickled.

3.3 Hypothesis 3 (age effects)

In this section of the study, I tested the hypothesis that age affects the presence and frequency of play faces and vocalizations in orangutans. All of the subjects in this study were considered infants according to the life stages already established by Watts and Pusey (1993): infants (0–4 years), juveniles (4–9 years), and adults (9–12 years). The infant orangutan subjects were divided into three mixed-sex groups: 13–24 months (N=7), 25–36 months (N=8), and 37–48 months (N=6). Hereinafter, I will refer to these as age groups 1, 2, and 3, respectively.

3.3.3 Number of occurrences

Presence of play face versus non-play face

The results for the presence of play faces versus non-play faces for the various age groups are summarized in Table 3.7.

Table 3.7: Play face versus non-play face — age

Subject	PF	No PF	Total
Group 1			
11. Hayes	9	19	28
41. Erin	20	10	30
12. Egol	33	1	34
7. Dominic	46	28	74
9. Lear	55	74	129
15. Lodik	63	1	64
5. Glenda	15	3	18
Total	241	136	377
Group 2			
3. Pascal	78	3	81
10. Morgan	88	4	92
8. Roberta	78	100	178
13. Leslie	13	23	36
16. Monroe	52	27	79
21. Sidney	15	4	19
4. Salosa	64	2	66
29. Irene	49	3	52
Total	437	166	603
Group 3			
2. Tim	19	28	47
6. Darren	20	1	21
27. Ade	14	0	14
33. Roy	7	2	9
1. Dr. Ann	8	2	10
23. Omry	41	0	41
Total	109	33	142
Grand Total	787	335	1122

Sub-dividing the sample by age did not alter the finding that play faces were more common than non-play faces. Play faces were two to three times more common than non-play faces in all three age groups (age group 1: 241 vs 136; age group 2: 437 vs 166; age group 3: 109 vs 33).

Subdividing the sample by age also did not affect the finding that there was considerable inter-individual variation in whether or not an orangutan exhibited a play face in response to tickling. In group 1, the number of occurrences in each category remained relatively evenly distributed. The play faces ranged from 9–63 whereas the non-play faces ranged from 1–74. Group 2 exhibited play faces in the highest numbers, were three times more likely to produce a play face than a non-play face and occurrences ranged anywhere from 13–88 for the play faces and from 2–100 for the

non-play faces. Group 3 had the lowest numbers overall; While their play faces ranged from 7–41, most of the subjects in this group had very low occurrences of non-play faces at either 0–2, with one individual displaying this response 28 times.

Turning now to differences between age groups, age group 1 produced 33.6% (377/1122) of the total tickle responses. Of these, 64% (241/377) consisted of play faces while 36% (136/377) were non-play faces. Age group 2 produced 53.7% (603/1122) of the total tickle responses. Of these, 72% (437/603) were play faces and 28% (166/603) were non-play faces. Age group 3 produced 12.7% (142/1122) of the total tickle responses. Of these, 77% (109/142) were play faces and 23% (33/142) were non-play faces. According to this data, the frequency with which individuals responded to tickling with a play face appeared to increase slightly with age.

In this section where I was testing whether age affected the presence of play faces among orangutans, it was found that overall play faces were more common than non-play faces. This was especially so for age group 2 which revealed the most play faces by the most individuals and in the highest numbers, which were three times higher than the non-play faces. Thus, there appears to be some evidence that age affected response to tickling such that older individuals are more likely to exhibit a play face than a non-play face, although this relationship only appears to exist between groups 1 and 2.

To test the above, I first conducted the chi-squared test. The χ^2 value for the groups was 0.08. The minimum significant χ^2 value for p=0.05 at 2 degrees of freedom was 5.99. As such, the hypothesis was not supported: No age group exhibited a play face significantly more than the other age groups.

To further examine the relationship between orangutan age and the presence of play face, Spearman's Correlation Coefficient was used. It indicates little to no correlation between these two variables when both the raw (r=-.212; p=.355) and the percentage data (r=.308; p=.174) were considered. Because these results were not statistically significant, I concluded that age does not appear to affect the likelihood of a play face response to tickling.

Play face types

The results for the presence and frequency of the four play face types for the three age groups are summarized in Table 3.8.

Table 3.8: Play face types — age

Subject	PF 1	PF 2	PF 3	PF 4	Total
Group 1					
11. Hayes	1	3	3	2	9
41. Erin	0	0	20	0	20
12. Egol	0	0	32	1	33
7. Dominic	0	2	34	10	46
9. Lear	0	0	36	19	55
15. Lodik	0	0	19	44	63
5. Glenda	1	0	11	3	15
Total	2	5	155	79	241
Group 2					
3. Pascal	0	8	47	23	78
10. Morgan	1	19	67	1	88
8. Roberta	1	1	70	6	78
13. Leslie	1	0	10	2	13
16. Monroe	0	2	49	1	52
21. Sidney	0	1	12	2	15
4. Salosa	1	5	53	5	64
29. Irene	2	0	47	0	49
Total	6	36	355	40	437
Group 3					
2. Tim	0	6	13	0	19
6. Darren	0	3	16	1	20
27. Ade	0	0	13	1	14
33. Roy	0	0	6	1	7
1. Dr. Ann	1	1	5	1	8
23. Omry	0	0	40	1	41
Total	1	10	93	5	109
Grand Total	9	51	603	124	787

Sub-dividing the sample by age did not alter the finding that PF 3 was much more common than the other play faces. It made up 77% (603/787) of the total play faces for all groups, 64% (155/241) of the total play faces for group 1, 81% (355/437) of the total play faces for group 2, and 85% (93/109) of the total play faces for group 3. Overall, the PF 3 made up 64–85% of the total play faces across all age groups, was exhibited by all individuals in all of the age categories, and was two to nine times higher than the second most common play face type in each group (Group 1: 155 vs 79; Group 2: 355 vs 40; Group 3: 93 vs 10).

Sub-dividing the sample by age also did not affect the finding that there was considerable inter-individual variation in terms of the play faces exhibited when an orangutan responds to tickling. For group 1, PF 1 and PF 2 were displayed between

0–3 times while PF 3 ranged between 3–36 and PF 4 between 0-44. Only one individual exhibited all four play faces but in very small numbers (1–3). Group 2 revealed much of the same exhibiting PF 1 between 0–2 times, PF 2 between 0-19, PF 3 between 10-70 and PF 4 between 0–23. Three individuals in this group produced all four play faces and have three of the highest total numbers of play faces overall. Group 3 had the lowest numbers: PF 1 and PF 4 were only seen 0–1 times, PF 2 was seen between 0–6, and PF 3 between 5-40. In this group, only one individual exhibited all four PF types.

Turning now to the differences between age groups, group 2 made up 59% of the total PF 3 for all age groups (355/603). They were followed by group 1 who made up 26% (155/603) of the total PF 3 for all age groups, and then group 3 at 15% (93/603). When comparing the other play faces in this same manner, there was no consistency or pattern with the exception of PF 4 where its frequency appears to decrease with age.

To test the above, first the chi-squared test was used. There were five cases in group 1, eight cases in group 2, and five cases in group 3 in which a PF 3 occurred more often than a PF 1, PF 2, or PF 4. As a result, the frequency of the PF 3 was compared among the age groups. The χ^2 value for this play face type was 0.19. The minimum significant χ^2 value for p=0.05 at 2 degrees of freedom was 5.99. As such, the hypothesis was not supported: None of the age groups exhibited a PF 3 significantly more often than the others.

To further examine the relationship between orangutan age and the presence and frequency of the four different play faces, Spearman's Correlation Coefficient was calculated. It indicated little to no association for play face types 1-3 when both the raw and the percentage data were analyzed (PF 1 Raw: r=-.059; p=.8; PF 1 Percent: r=-.085, p=.715; PF 2 Raw: r=.105; p=.652; PF 2 Percent: r=.142; p=.540; PF 3 Raw: r=-.057; p=.806; PF 3 Percent: r=.196; p=.395). In terms of PF 4, however, Spearman's Correlation Coefficient indicated a possible weak negative association for both the raw (r=-.378; p=.091) and percentage data (r=-.340; p=.131). Because none of these observations were statistically significant, I concluded that age does not appear to affect the presence or frequency of a play face when an orangutan responded to tickling with a play face.

Silent versus Vocal Play faces

This section looked specifically at the number of play faces that were produced with a vocalization. It was found that sub-dividing the sample by age did not affect the finding that there was considerable inter-individual variation in terms of whether or not a play face was accompanied by a vocalization in response to tickling. The results for the presence of vocalized versus silent play faces are presented in Table 3.9 wherein the four play face types are combined. With age group 1, all seven individuals produced both silent and vocalized play faces, which ranged from 4–59 and 2–23, respectively. The majority of subjects in this group (5/7) produced a higher number of silent play faces than vocalized ones with one individual producing an equal number of both. In age group 2, all eight individuals produced both silent and vocal play faces which ranged from 9–76 and 2–47, respectively. Within this group, again, most subjects (6/8) were more likely to produce a higher number of silent play faces. With age group 3, only four out of six individuals produced both the silent and vocalized play faces, which ranged from 3–38 and 0–7, respectively. Only one individual had a higher number of vocalized play faces with five out of six subjects producing more silent play faces.

Overall, not only were the silent play faces more common than the vocalized play faces, the ranges were also much larger for all three age groups.

Turning now to the differences between age groups, age group 2 produced the most vocal play faces at 63% (126/199) out of the total number of vocal play faces for all age groups. Silent play faces made up 71% (311/437) of total play faces for this group which was two and a half times higher than the vocal play faces. Age group 1 produced the second highest number of vocal play faces (57/199) making up 29% of the total number of vocal play faces for all age groups. Silent play faces made up 76% (184/241) of total play faces for this group, which was three times higher than the vocal play faces. Age group 3 was last in terms of the total number of vocal play faces, producing only 8% (16/199) of the total vocal play faces for all age groups. However, they had the highest percentage of silent play faces at 85% (93/109) of total play faces for this group, making the silent play faces six times higher than the vocal.

Table 3.9: Silent versus vocalized play faces — age

Subject	Silent PF	Vocal PF	Total
Age Group 1			
11. Hayes	4	5	9
41. Erin	14	6	20
12. Egol	24	9	33
7. Dominic	23	23	46
9. Lear	47	8	55
15. Lodik	59	4	63
5. Glenda	13	2	15
Total	184	57	241
Age Group 2			
3. Pascal	76	2	78
10. Morgan	41	47	88
8. Roberta	43	35	78
13. Leslie	9	4	13
16. Monroe	49	3	52
21. Sidney	9	6	15
4. Salosa	60	4	64
29. Irene	24	25	49
Total	311	126	437
Age Group 3			
2. Tim	12	7	19
6. Darren	20	0	20
27. Ade	14	0	14
33. Roy	3	4	7
1. Dr. Ann	6	2	8
23. Omry	38	3	41
Total	93	16	109
Grand Total	588	199	787

Overall, silent play faces were much more common than the vocalized, making up between 76–85% of the total play faces for each group, and being 2.5–6 times higher than the vocalized play faces. Age group 2 had the highest number of vocalized play faces, followed by group 1 with group 3 tailing far behind with next to no vocalized play faces at all. As a result, age did not appear to be a factor in affecting whether a subject would exhibit a vocalized or silent play face when tickled.

Overall, group 2 made up 53% (311/588) of the total silent play faces for all age groups, 63% (126/199) of the total vocal play faces for all age groups, and 56% (437/787) of all play faces (both silent and vocal) for all the age groups. Age group 1 and then age group 3 followed. As such, age did not appear to be a factor that affected the type of silent or vocal play face exhibited.

My intention was to use the chi-squared analysis to test the above with both the silent and vocalized play face responses. However, calculations were not necessary for the latter as there were no cases in which a vocalized play face occurred significantly more frequently than a silent play face for any group. For the silent play face, the χ^2 value for this response was 0.08. The minimum significant χ^2 value for p=.05 at one degree of freedom was 3.84. As such, the hypothesis was not supported. Some orangutans emitted vocalizations while exhibiting play faces, but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. In addition, no age group exhibited a silent play face significantly more than any other age group.

To further analyze if age affects whether play faces will be accompanied by a vocalization or not, Spearman's Correlation Coefficient was calculated. It indicated little to no association for the silent play face when both the raw data (r=-.160; p=.489) and the percentage data (r=.194; p=.398) were analyzed. This was also the case for the vocal play face percentage data (r=-.194; p=.398). There was, however, a possible weak negative correlation for the vocal play face raw data (r=-.384; p=.085). Because all of these correlations were not statistically significant, I concluded that age was not a factor in affecting whether an orangutan would exhibit a vocal or silent play face when tickled.

3.4 Hypothesis 4 (time effects)

In this section of the study, I tested the hypothesis that the length of time an orangutan has spent in rehabilitation at the Care Centre affects the presence and frequency of play faces and vocalizations among orangutans when tickled. The subjects were divided into three categories, regardless of age or sex, based on the number of months they had been at the Care Centre: 0–12m (N=6); 13-24 (N=12), 25–42m (N=3). Hereinafter, I will refer to these groups as time groups 1, 2, and 3, respectively.

3.4.4 Number of occurrences

Presence of play face versus non-play face

The results of the presence of play face versus non-play face for the various time groups are summarized in Table 3.10.

Sub-dividing the sample by time spent in rehabilitation at the Care Centre did not affect the findings that play faces were more common than non-play faces. Play faces were one to ten times more frequent than non-play faces in all three time groups (Group 1: 173 vs 17; Group 2: 573 vs 285; Group 3: 41 vs 33).

Sub-dividing the sample by time also did not affect the finding that there was considerable inter-individual variation in whether or not an orangutan exhibited a play face in response to tickling. Within group 1, the play faces were ten times more likely to occur than the non-play faces. The lowest number of occurrences was eight but the rest were produced between 10–78 times. Conversely, the non-play faces were only exhibited by one individual ten times but the majority only 0–3 times. Group 2 produced play faces in the highest numbers and was twice as likely to exhibit a play face than a non-play face. Three individuals produced a play face 9–13 times whereas the majority of the subjects in this group displayed it between 41 and 88 times. The range for the non-play faces was more extreme, ranging from 0–100. While group 3 had the lowest total responses, with both the play face and non-play face totals being relatively equal, the range for play faces was 7–19 while the non- play faces was 2–28.

Turning now to differences between time groups, time group 1 produced 17% (190/1122) of the total tickle responses. Of these, 91% (173/190) consisted of play faces while 9% (17/190) were non-play faces. Time group 2 produced 76% (858/1122) of the total tickle responses. Of these, 67% (573/858) were play faces and 33% (285/858) were non-play faces. Time group 3 produced 7% (74/1122) of the total tickle responses. Of these, 55% (41/74) were play faces and 45% (33/74) were non-play faces. Thus, using this data, the frequency with which individuals respond to tickling with a play face decreases with the amount of time spent in rehabilitation at the Care Centre.

In this section where I tested whether time spent at the Care Centre affected the presence of play face responses among orangutans, overall it was found that play faces were more common than the non-play faces. However, while play faces were ten times higher than non-play faces within group 1, group 2 revealed the highest number of play faces with an average of 52, and group 3 had very low frequencies in comparison to the others. There were no other obvious patterns. As a result, it initially appeared that time does not have an effect on the presence and frequency of play faces in response to tickling. In contrast, when the percentage of play faces was considered out of the total number of tickle responses for each group, time did appear to be a factor. As outlined in the above paragraph, the percentage of play faces for

groups 1-3 respectively are 91, 67, and 55%. As a result, it initially appeared that the likelihood of a play face response decreased with the time spent at the Care Centre.

Table 3.10: Play face versus non-play face — time

Subject	PF	No PF	Total
Time Group 1			
27. Ade	14	0	14
41. Erin	20	10	30
3. Pascal	78	3	81
6. Darren	20	1	21
12. Egol	33	1	34
1. Dr. Ann	8	2	10
Total	173	17	190
Time Group 2			
7. Dominic	46	28	74
29. Irene	49	3	52
10. Morgan	88	4	92
11. Hayes	9	19	28
13. Leslie	13	23	36
15. Lodik	63	1	64
23. Omry	41	0	41
4. Salosa	64	2	66
9. Lear	55	74	129
16. Monroe	52	27	79
8. Roberta	78	100	178
21. Sidney	15	4	19
Total	573	285	858
Time Group 3			
33. Roy	7	2	9
5. Glenda	15	3	18
2. Tim	19	28	47
Total	41	33	74
Grand Total	787	335	1122

To test the above, first the chi-squared test was used. The χ^2 value for the groups was 0.08. The minimum significant χ^2 value for p=0.05 at two degrees of freedom was 5.99. As such, the hypothesis was not supported: No time group exhibited a play face significantly more than the other time groups.

To further examine the relationship between the length of time an orangutan has spent in rehabilitation and the presence of play faces, Spearman's Correlation Co-efficient was then calculated. It indicated that while there was little to no correlation between these two variables when the raw data was considered (r=-.114, p=.624),

there was a possible weak association when the percentage data was analyzed (r=-.378, p=.092). However, because these results were not statistically significant, it was concluded that time spent in rehabilitation at the Care Centre did not affect the likelihood of a play face response to tickling.

Frequency of play face types

The results for the presence and frequency of the four play faces for the three time groups are presented in Table 3.11. Sub-dividing the sample by the length of time spent in rehabilitation at the Care Centre did not alter the finding that PF 3 was much more common than the other play faces. More specifically, PF 3 made up 77% (133/173) of the total play faces for group 1 and group 2 (440/573), and 73% (30/41) for group 3. Therefore, PF 3 made up 73-77% of the total play faces across all time groups. In addition, PF 3 was the only play face type exhibited by all subjects in all three time groups and was much higher in frequency than the other play faces. In fact, it was five times greater than the second most common play face in each group. The ratios were as follows: Group 1: 133 vs 27; Group 2: 440 vs 93; Group 3: 30 vs 6).

Sub-dividing the sample by age also did not affect the finding that there was considerable inter-individual variation in terms of the play face types exhibited when an orangutan responded to tickling with a play face. For group 1, PF 1 was only displayed once, PF 2 between 0–8 times and PF 4 was exhibited by the majority of subjects between 0–1 times but one individual produced a PF 4 eight times. PF 3 on the other hand revealed a much higher range between 5–47. Only one subject exhibited all four play faces but in small numbers (1–5). Group 2 revealed a similar order of decreasing occurrences but the range of differed slightly. PF 1 was seen between 0–2 times, PF 2 between 0–19, PF 3 between 3–70, and PF 4 between 0–44 times. Four individuals produced all four play faces. Group 3 had the lowest numbers: PF 1 was seen 0–1 times, PF 2 between 0–6, PF 3 between 6–13, and PF 4 between 0–3. No individual in this group produced all four play faces. Thus, it can be seen that the inter-individual variation among the time groups was great.

Turning now to the differences between time groups, group 2 had the highest number of PF 3 making up 73% (440/603) of the total PF 3 for all time groups; They were followed by group 1 at 22% (133/603) with group 3 in last place at 5% (30/603). When comparing the other play faces in this same manner, they all revealed a similar pattern, decreasing in frequency from group 2 to group 1 to group 3. As a result, it appears that time does not appear to be a strong factor in predicting which type of play face will be displayed by an orangutan when tickled.

Table 3.11: Play face types — time

Subject	PF 1	PF 2	PF 3	PF 4	Total
Time Group 1					
27. Ade	0	0	13	1	14
41. Erin	0	0	20	0	20
3. Pascal	0	8	47	23	78
6. Darren	0	3	16	1	20
12. Egol	0	0	32	1	33
1. Dr. Ann	1	1	5	1	8
Total	1	12	133	27	173
Time Group 2					
7. Dominic	0	2	34	10	46
29. Irene	2	0	47	0	49
10. Morgan	1	19	67	1	88
11. Hayes	1	3	3	2	9
13. Leslie	1	0	10	2	13
15. Lodik	0	0	19	44	63
23. Omry	0	0	40	1	41
4. Salosa	1	5	53	5	64
9. Lear	0	0	36	19	55
16. Monroe	0	2	49	1	52
8. Roberta	1	1	70	6	78
21. Sidney	0	1	12	2	15
Total	7	33	440	93	573
Time Group 3					
33. Roy	0	0	6	1	7
5. Glenda	1	0	11	3	15
2. Tim	0	6	13	0	19
Total	1	6	30	4	41
Grand Total	9	51	603	124	787

To test the above, first the chi-squared test was used. There were five cases within group 1, ten cases in group 2, and three cases in group 3 in which a PF 3 occurred more often than a PF 1, PF 2, or PF 4. As a result, the frequency of the PF 3 was compared among the time groups. The χ^2 value for this play face type was 0.03. The minimum significant χ^2 value for p=0.05 at two degrees of freedom was 5.99. As such, the hypothesis was not supported: None of the time groups exhibited a PF 3 significantly more often than the others.

To further examine the relationship between the time an orangutan had spent at the Care Centre with the presence and frequency of the four different play faces, Spearman's Correlation Coefficient was calculated. It indicated little to no association for all play faces when both the raw and the percentage data were considered [PF 1

Raw: r=.081, p=.728; PF 1 Percent: r=.064, p=.783; PF 2 Raw: r=-.002, p=.994; PF 2 Percent: r=.004, p=.986; PF 3 Raw: r=-.059, p=.799; PF 3 Percent: r=-.147, p=.524; PF 4 Raw: r=.152, p=.512; PF 4 Percent: r=.089, p=.700].

In sum, then, it appeared that time spent in rehabilitation at the Care Centre did not affect the presence or frequency of a specific play face type response, in this case a PF 3.

Silent versus vocal play faces

This section looked more specifically at the number of play faces that were produced with a vocalization. It was found that sub-dividing the sample by time spent in rehabilitation did not affect the finding that there was considerable inter-individual variation in terms of whether play faces were accompanied by a vocalization in response to tickling. The results for the presence of vocalized versus silent play faces are presented in Table 3.12 wherein the four play faces are combined. With group 1, four out of six subjects produced both silent and vocal play faces whose respective ranges were between 6–76 and 0–9. This group revealed that when an individual produced a play face, it would more frequently be silent. Within group 2, all 12 individuals exhibited both types of play face which ranged from 4–60 for the silent and between 3–47 for the vocalized play faces. Only three subjects in this group produced a higher number of vocalized play faces than silent play faces and one subject had equal numbers of both. However, most individuals in this group were more likely to exhibit a higher number of silent play faces. With group 3, all three individuals produced both play faces and only one of those had a higher number of vocalized versus silent with numbers ranging between 2–7 and 3–13, respectively. Therefore, all three groups produced silent play faces in much greater frequency than the vocalized play faces.

Turning now to the difference between groups, group 2 produced the most vocalized play faces at 84% (167/199) out of the total number of vocal play faces for all groups. Silent play faces made up 71% (406/573) of the total play faces for this group which was two and a half times higher than the vocalized play faces. Group 1 produced the second highest number of vocalized play faces (19/199) making up 10% of the total number of vocal play faces for all groups. However, they exhibited the highest percentage of silent play faces, making up 89% (154/173) of the total play faces for this group which was eight times higher than the vocal play faces. Group 3 was last in all respects. In terms of the total number of vocalized play faces, they made up 6% (13/199) of the total vocal play faces for all three groups. Their silent play faces

made up 68% (28/41) of the total play faces for this group which was over two times higher than the vocalized.

Table 3.12: Silent versus vocalized play faces — time

Subject	Silent play face	Vocal play face	Total
Time Group 1			
27. Ade	14	0	14
41. Erin	14	6	20
3. Pascal	76	2	78
6. Darren	20	0	20
12. Egol	24	9	33
1. Dr. Ann	6	2	8
Total	154	19	173
Time Group 2			
7. Dominic	23	23	46
29. Irene	24	25	49
10. Morgan	41	47	88
11. Hayes	4	5	9
13. Leslie	9	4	13
15. Lodik	59	4	63
23. Omry	38	3	41
4. Salosa	60	4	64
9. Lear	47	8	55
16. Monroe	49	3	52
8. Roberta	43	35	78
21. Sidney	9	6	15
Total	406	167	573
Time Group 3			
33. Roy	3	4	7
5. Glenda	13	2	15
2. Tim	12	7	19
Total	28	13	41
Grand Total	588	199	787

Overall, silent play faces were much more common than the vocalized, making up between 68-89% of the total play faces for each group, and being two to eight times higher in frequency than the vocalized play faces. Group 2 had the largest numbers of vocalized play faces which was followed by group 1 while group 3 closely behind that. As a result, time spent in rehabilitation at the Care Centre does not appear to be a contributing factor in affecting whether an orangutan subject will exhibit a vocalized or silent play face in response to being tickled.

In sum, group 2 made up 69% (406/588) of the total silent play faces for all three groups, 84% (167/199) of the total vocal play faces for all three groups, and 73% (573/787) of all play faces (both silent and vocal) for all three groups. The other time groups did not have similarly impressive numbers nor follow in any predictable order or pattern. Thus, time spent in rehabilitation at the Care Centre did not appear to affect the type of silent or vocal play face exhibited by orangutans in response to tickling.

My intention was to use the chi-squared analysis to test the above with both the silent and vocalized play face responses. However, calculations were not necessary for the latter as there were no cases in which a vocalized play face occurred significantly more frequently than a silent play face for any group. For the silent play face, the χ^2 value for this response was 0.15. The minimum significant χ^2 value for p=.05 at one degree of freedom was 3.84. As such, the hypothesis was not supported: Some orangutans emitted vocalizations while exhibiting play faces, but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. In addition, no time group exhibited a silent play face significantly more than any other age group.

To further analyze if time spent at the Care Centre affects whether play faces would be accompanied by a vocalization or not, Spearman's Correlation Co-efficient was calculated. It indicated little to no correlation for both silent and vocal play faces when both the raw (Silent PF: r=-.111, p=.631; Vocal PF: r=.179, p=.438) and the percentage data (Silent PF: r=-.287, p=.207; Vocal PF: r=.287, p=.207) were considered. Because all of these correlations were not statistically significant, one can conclude that time spent in rehabilitation at the Care Centre was not a factor in affecting whether or not an orangutan would produce a vocalization in association with play faces when tickled.

Chapter 4
Discussion

4.1 Summary of results

In the study reported here, I investigated whether orangutans engage in laughter behaviour. To do so, I recorded the presence and frequency of facial expressions and vocalizations in response to tickling, seeking evidence of play faces co-occurring with vocalizations, and thus, the potential for laughter. In the first analysis, I considered the entire sample. Subsequently, I carried out analyses in which I controlled for sex, age, and time spent in rehabilitation at the Care Centre. The analyses indicated that when tickled, orangutans exhibit play faces significantly more often than non-play faces and silent play faces more frequently than vocalized play faces. Sex, age, and time in rehabilitation did not affect these findings. The study also found that while some orangutans emitted vocalizations while exhibiting play faces, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. Therefore, this study was unable to support the hypothesis that orangutans laugh.

4.2 Potential limitations of the study

At both the data collection and analytical phases of this study, there are several factors that could have affected my results. These potential shortcomings are discussed below.

4.2.1 Data collection

During the data collection stage in the field, I encountered a number of difficulties. These relate to subject selection, location of recording, tickling as a stimulus, and video recording.

Subject selection

The first problem during the data collection stage was subject selection. On half of the occasions, orangutans were chosen as subjects either by myself or a caregiver. Using this method, results could have been affected by an individual feeling forced into a situation with a caregiver/assistant with which they were unfamiliar or into an interaction when they were not in the mood to play. Due to these factors, the tickling session would not be enjoyable and would be unlikely to induce laughter. On the other half of the occasions, episodes were recorded when orangutans initiated contact with a caregiver, and tickling interactions ensued. While preferable, these sessions also had their drawbacks. For example, these recordings were initiated by playful, outgoing, healthy, and relaxed orangutans who, from the onset, may have been more likely to play and laugh due to their personality. The fact that these subjects were choosing to play and be tickled could have caused very different responses than those responses from orangutans chosen via the first method who were possibly more shy, ill, tired, moody, or uncomfortable and ultimately forced into such an interaction.

To address this subject selection issue, I tried changing the context of tickling to natural play, which allowed for more spontaneity. Several hours were recorded using this method but it was rejected for a number of reasons. First, natural play often occurred far off in the distance, in water, or high up in the trees where accurate recordings were unobtainable. Second, such play often involved more than just two individuals, with the dynamics and members changing frequently during one play bout. This made it difficult to record faces directly or to determine who was vocalizing at any given time. The third reason natural play contexts were not examined was due to my lack of experience working with these orangutans. Identifying the subjects involved in the more controlled tickling sessions involved a high degree of familiarity with these animals. Therefore, subject identification would have been even more difficult during natural play when orangutans are in close contact, physically entangled, and often at great distances. I was not in the field long enough to acquire this ability, and while the caregivers could identify individuals in close proximity, accuracy diminished with distance. In the end, the least biased results were obtained by choosing orangutans on certain occasions while allowing orangutans to choose their participation in other sessions.

Another issue with subject selection was that, due to a lack of time and personal safety issues, my study was restricted to infant orangutans. One potential explanation for the fact that I did not discover a significant amount of vocal laughter in response to tickling is that perhaps this form of laughter emerges later in life in

orangutans. A second explanation could be that vocalizations co-occur with play faces at high rates only in situations of very high play intensity. In order to test the effects of age, I considered examining the potential existence of laughter among additional age groups. However, while this would have been informative, the use of older and more mature orangutans was rejected. This was based partly on the fact that it would have been more difficult and potentially dangerous for females to work with male subjects reaching sexual and physical maturity. In fact, for reasons of personal safety, the caregivers responsible for the older orangutans at the care centre were male. Compounded with this issue of strength and maturity, regardless of sex, it would have been extremely difficult to persuade these stronger and more independent orangutans into a situation in which they could be tickled and recorded. Under the conditions of this study, the option of using additional age groups was not possible but leaves opportunities for future studies to examine laughter among juvenile orangutans.

A final problem with subject selection was the fact that many of the orangutans utilized in this study were individuals who had just recently arrived at the Care Centre. In addition, all of them (except one who was born at the centre) would have been removed from their mothers and natural habitats, often violently, to be later confined in conditions where they were likely socially, emotionally, and physically abused from a very young age. It is possible that the physical and psychological effects of their experiences could produce both short and long-term damage to the point that these individuals could not reach a physiological state necessary for the production of laughter regardless of the stimulus. While this raises the potential concern for using rehabilitated orangutans as subjects, I do not feel that their use undermines the results of this study at all. In fact, evidence of play behaviours and play faces were discovered, and significantly so. In addition, although not statistically significant, play vocalizations were also observed among these subjects. As a result, the rehabilitated orangutans in this study seemed to be an adequate sample and did not appear to jeopardize the final results.

In the end, the potential problems surrounding subject selection appear minimal and I do not think they affected the validity of my results. This is because subject selection was undertaken as objectively as possible and produced a variety of responses likely representative of a larger orangutan population.

Location selection

The second potential problem during the data collection stage was the lack of a single recording location. Originally I considered using one location for recording all tickle

sessions. However, once I arrived in the field, it was quickly realized that this would not be feasible. However, under specific circumstances, when recording in the open forest was not possible (i.e., rainy days), the default location became the play station at Pondok Waru. While this location allowed me to record one individual at a time under the same controlled conditions and without other orangutan disruption, it had its drawbacks. These interactions seemed forced and unnatural for the caregivers and the subjects who were brought from their sleeping quarters unexpectedly to a platform not normally utilized for play or other orangutan activities. In addition, this platform was covered with a tin roof that amplified the sound of rain, which made it difficult to acquire adequate sound recordings. This location did not produce many recordable responses.

In the end, tickle episodes were recorded in different locations depending on the group of orangutans — where they were housed is based on the time they have spent in rehabilitation — in addition to factors like the weather and day of the week (i.e., Sunday they do not go into the rainforest). As a result, inconsistency in regards to location may have affected the overall results because it caused other factors to become uncontrolled. In addition to swamp water, which occasionally obstructed my ability to get close enough to obtain a recording or disrupted the focal sounds being recorded as other orangutans splashed around, these variables included rain, trees, limited amount of space for playing and recording, inability to restrict the involvement of others orangutans, or other uncontrollable distractions that caused sound and video interference.

Despite these potential problems, the use of the various locations depending on the circumstances and the group of orangutans being observed at the time proved to be most successful. This is because orangutans were recorded in areas where they felt most comfortable and where they played and interacted on a regular basis. These locations seemed to be the most conducive to creating a playful and laughter-inducing atmosphere if laughter was indeed going to be produced and thus, did not appear to invalidate the results of this study.

Tickling as a stimulus

As discussed in the Materials and Methods chapter, tickling was chosen as the most appropriate laughter-inducing stimulus in this study for a number of reasons: its role in social play among non-human primates, its frequent use in prior laughter research (as already discussed), the fact that some great apes and humans appear to share the same ticklish regions of the body (Provine 2000; van Lawick-Goodall 1971), and its

reliability for producing similar vocal and facial responses in both chimpanzees and humans (Provine 1996, 2000; Vettin and Todt 2005). Tickling also allowed me to quickly and systematically test a large sample of individuals over a relatively short period of time.

For the reasons listed above, tickling presented itself as being the most reliable means for evoking laughter if it was to exist among orangutans. However, it did raise some potential problems: Tickling is subjectively enjoyable depending on the relationship between those involved, the mood/health/personality of the ticklee, and the vigor of the tickle. It is possible that my study did not produce the strong association between play faces and vocalizations predicted by the vocal laughter hypothesis because of these reasons. However, the fact that the majority of the tickle sessions involved a healthy, playful and consenting orangutan subject, the possible shortcomings raised by this method did not appear to ultimately affect the end results. In fact, these tickling bouts often escalated into rough and tumble social play which indicated to me that the orangutan subjects were enjoying the interaction, and if laughter was going to be produced, it would most likely occur under these circumstances.

Other issues that may have influenced the results of my study pertain to the ticklers themselves. Two individuals were employed as ticklers in the majority of the encounters. These two caregivers were also my translators and were chosen for these roles due to our rapport, their work ethic, their reliability, and their overall comprehension of the study. More importantly, the two individuals had close relationships with most of the orangutans and their personalities were playful, friendly, gentle, and energetic, qualities that seemed to be best suited to the research. In addition, these caregivers had similar play styles. This allowed me to utilize them for most interactions while maintaining a consistent tickling stimulus across the study.

However, restricting the ticklers to only two individuals raised some concerns. For example, there were a few orangutans who did not know these staff-members as well as other staff-members, especially within the first age group who had not been at the OQCC for long and were shyer and somewhat more inhibited. This could have resulted in fewer laugh responses because tickling is a social activity, one that requires an intimate relationship between the tickler and ticklee. To address this issue, I occasionally substituted one of my main assistants and employed a different caregiver with whom the orangutan was more familiar. Theoretically, the problem of tickler selection could have affected this study causing fewer laugh responses among the younger orangutans. However, this does not appear to be the case. In fact, age groups

one and two produced silent and vocalized play faces more frequently than age group three who had been at the care centre for the longest period of time. As such, it seems unlikely that restricting the use of the two main ticklers negatively impacted the validity of my results.

Video and sound recording

The final major problem area in the data collection portion of my study pertains to the technical obstacles concerning sound recording equipment. It was difficult to keep the microphones out of the subject's reach yet close enough to obtain an accurate sound recording. Because orangutan vocalizations are most audible at very close distances, microphones needed to be close to the orangutan's mouth while simultaneously not distracting them from the interaction. It was also a challenge to keep other orangutans from entering the tickle/play episode being recorded especially among the youngest group where sometimes several orangutans would be trying to play with the orangutan being tickled, the tickler, or the videographer. Although I originally used a hand-held boom microphone, because it was often bumped or pulled, it was always being moved to avoid such situations. This affected the recordings. To deal with this issue, I found a lapel microphone worked best. This was because it could be most easily and quickly removed if orangutans attempted to grab it, it was the least distracting to the subject, and an assistant could dangle it in close proximity to the subject's mouth, providing me with the clearest recordings. While alternative options will be discussed later in this chapter, the microphone dilemma presented itself as a minor problem in the field but one that was quickly rectified. Ultimately, the methods used captured sound and video recordings with audible vocalizations and clear facial expressions that proved useful during data analysis.

4.2.2 Data analysis

The data analysis portion of the study had its share of problems too. There are five in particular that require addressing. They involve the selection of tickle episodes to analyze, identification and categorization of age and time in captivity, identification and categorization of play and non-play faces, identification of vocalizations, and lack of inter-observer reliability.

Selection of tickle episodes to analyze

During the analytical phase of my research, the first problem I encountered was how to quantify the data collected. This step was required in order to deal with the fact that some individual orangutans had multiple recordings while others had only one. The first solution considered was to calculate the average for those orangutans that had multiple recordings. This was rejected on the grounds that it would skew the results, because it would result in some individuals being over-represented. The second solution was to take all episodes lacking co-occurring play faces and vocalizations versus those episodes that did contain co-occurring play faces and vocalizations and randomly select one out of the multiple sequences for that particular individual. This was also rejected to avoid some individuals being over-represented. The third option considered was to treat all tickle episodes for one individual as a single data point. This was rejected on account of the huge time constraint it would have added to the analytical portion of this study. In the end, the problem was solved by randomly selecting one tickle bout per individual only.

The method of random selection raises two major concerns. The first is that although one orangutan may have produced a laugh-like response several times or on one occasion, if this episode was not the episode randomly selected for analysis, it could under-represent the fact that orangutans produce laughter. In fact, based on personal observation, play vocalizations similar to that found in other great apes as described by other primate researchers in the literature, orangutans were heard play vocalizing in this context. However, because this study was limited to the tickle samples randomly selected, I was unable to statistically support the existence of orangutan laughter as defined by this study.

In addition, those orangutans that were recorded several times due to their desire to play or interact with the human caregivers based on certain characteristics (i.e., mood, health, personality) were probably more likely to emit laugh-like vocalizations in general. Therefore, the odds of randomly selecting an episode where these subjects produced a laugh response would have been higher. This would have been based on personality and the fact that they were recorded numerous times, increasing their level of familiarity and comfort with the tickler and the situation. Conversely, those that were shyer, more timid, younger or sick might have been only recorded once. Thus, based again on their personality traits, some orangutans would not become as familiar with the situation or the ticklers, causing them to be less likely to produce laugh-like responses. Both of these scenarios could have skewed the results to some extent. However, random selection appeared to be the best means for

maintaining objectivity and controlling for skewness, while still acquiring an adequate sample of responses most reflective of a larger population.

Identification and categorization of age and time groups

Another potential problem has to do with cross-sectional analysis and the identification of orangutan ages. First, the ages of the orangutans in my study were estimated in months and provided to me by the veterinarians at the OCCQ. Because the orangutans were not born at the Care Centre (except for one) and had been brought to the centre from various sources/locations, their personal histories are unknown. As a result, their ages were approximated based on other means (i.e., teeth, weight). Second, it is difficult to find one standard framework of what ages constitute a juvenile and that of an infant. While Mastusaka (2004) defines infants as zero to three yeas of age and juveniles from four to seven years, the majority of studies define infants as zero to four years of age (e.g., Hiraiwa-Hasegawa et al. 1984; Nishida et al. 1990). Because all orangutan subjects used in this study were four years old or younger, I decided to classify the orangutans in this study based on the latter scheme. As a result, this study became an examination of laughter among infant orangutans only.

The potential problem with this categorization is that the identification of an orangutan as an infant or a juvenile is somewhat subjective and involves a very narrow window of time, sometimes only a month or even days. As such, this categorization choice could have affected the interpretation of results and raises a number of important questions: Could I have grouped the subjects differently when analyzing the variable of age? Was I only dealing with infants or a combination of both? Were the orangutans that produced laugh-like responses most frequently infants or juveniles, and how does this affect my final conclusions? Do the age categories explain why I did not see as much laugh-like behaviour as I had expected and would my conclusions about the effects of age on the co-occurrence of play faces and vocalizations been different had I grouped them differently?

In answer to the above questions, I feel the age categories were sufficient and did not undermine my results. If I had chosen to use the schema put forth by Mastusaka (2004), the four-year old orangutans would have been classified as juveniles. However, regardless of their age group title, their sample size would have remained exactly the same (n=3). Because this group only contained three individuals, it would have been difficult to draw concrete conclusions on the behaviour of the larger juvenile orangutan population based on the behaviours of only three individuals in my study. In addition, whether these orangutans were labeled older infants or young

juveniles, it does not change the fact that this group did not emit silent or vocalized play faces as much as the other age groups. In the end, the conclusion remains the same — age does not affect the way an orangutan responds to tickling.

Similar to the age groupings, I divided the subjects into three separate categories based on time spent at the rehabilitation centre. In doing so, I attempted to have three relatively equal sample sizes in order to compare data based on equal lengths of time at the centre (e.g., 12 month intervals). However, this method of categorization raises questions similar to those regarding age. Ultimately, did the way the groups were divided influence my conclusions about the effects of time on the co-occurrence of play faces and vocalizations? Would these conclusions have been different had I grouped the subjects according to different time intervals? For example, the time group 2 produced the most play faces. Hypothetically, I had considered moving three of the subjects who had been at the care centre for the longest period of time in group 2 and placing them in group 3. This would have created more equal sample sizes for comparison. If I had done it in this way, I may have concluded that time spent at the Care Centre does in fact affect the production of laugh-like behaviour, contradicting my current finding that time is not a factor. However, this is not the case. In the end, time group 2 still produced the most play faces. As such, the method of time categorization did not appear to invalidate the finding that time in rehabilitation does not effect the production of silent and vocalized play faces.

Identification and categorization of play and non-play faces

During the data analysis section of my study, I initially had to identify what constitutes a play face. As discussed in the Materials and Methods chapter, I arrived at four categories by compiling schemes previously established by other researchers (i.e., Matsusaka 2004; Ross 2007; Van Hooff et al. 2003). As a result, my play faces combined the three laugh variants (ROM, OMNT, OMBT) originally defined by Van Hooff and Preuschoft (2003), and the bite face, based on the findings of Matsusaka (2004). This play face can be described as starting out as either an OMBT or ROM but an attempt to bite is apparent. The tickler's hand or other body part is nearby and sometimes, actual contact occurs but generally it is simply a lunge or an attempt to bite. In general, though, it was extremely difficult to separate the bite face from the other play faces. This was also confirmed to be the case in Ross' (2007) study where she admitted to missing bite faces in her analysis due to the fact that during close bodily contact during tickling and social play, faces are difficult, if not impossible, to videotape. Therefore, I only included those bite faces that were easily identified as

separate from the other play faces and which co-occurred with a vocalization. Therefore, as with Ross' (2007) study, the number and duration of bite faces is likely under-represented in my study and definitely requires further investigation into its presence, frequency, and role in laughter.

The second problem associated with facial expression identification has to do with the large category of non-play faces. Due to personal inexperience in the identification of facial expressions in general, it is possible that play faces are being classified incorrectly and placed in the non-play face category accidently or that SBT displays were incorrectly classified as OMNT play faces. This raises questions about whether these non-play faces represent individual variation due to sex, age, length of time in rehabilitation or personality, and whether my results are due to the tickling context or the facial expression categories in general.

In defence of the identification system used, and despite my inexperience in facial analysis, I am confident that play faces were accurately identified as such. And even if SBT display were included in the OMNT play face categories, the effect on the end results would be minimal as few of these displays were produced overall. I am also aware that bite faces have been potentially under-represented in this study, however the overall effect on the results should also be insignificant. Play faces for all subjects, regardless of sex, age, and time in rehabilitation, were produced more frequently than non-play faces. If I had identified and included additional bite faces in the play face category, these numbers would simply become higher than they currently are, further supporting the study's findings. For this reason, the problems associated with play face identification do not appear to undermine my results.

Identification of vocalizations

The next problematic issue pertains to the identification of vocalizations. As indicated in the literature and experienced during my fieldwork, orangutan vocalizations are infrequent and barely audible unless within very close proximity. As a result, it is very possible that vocalizations emitted by some of the subjects were not captured during the data collection process, or they were not detectible during the analysis of the recordings. My results indicate that while some orangutans emitted vocalizations when exhibiting play faces, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfil the definition of laughter used in this study. Therefore, the hypothesis that orangutans laugh could not be supported. However, if these vocalizations are simply at a level that could not be detected by the equipment utilized or by the human ear, this does not mean they are not produced or not heard or

interpreted by other orangutans. As a result, vocal laughter could have been underrepresented, leading me to inaccurately conclude that laughter does not exist based on the definition used in this study. During the recording in the field, it was sometimes difficult to determine if vocalizations were being produced. However, when the results were being analyzed, the sound recordings were clear, audible, and easily recognized. As a result, I am confident that when vocal laughter was produced it was appropriately identified as such.

Inter-observer reliability

The final concern in regards to the validity of this study pertains to the lack of inter-observer reliability. As previously mentioned, I reviewed each tickle episode a minimum of twice for each orangutan subject. Due to ambiguities in either facial or vocalization identification, some occasions required further verification and were thus reviewed as necessary. However, one major improvement to this study would be to have all the categories identified and the results analyzed by a second or third researcher in addition to myself. Unfortunately, this was not possible. There are very few great ape researchers in Canada, with only a handful in the world who are currently studying orangutan laughter. Thus, a combination of lack of time, money, and feasibility prevented me from accounting for inter-observer reliability. From this, it is possible that play faces, non-play faces, and vocalizations have been categorized or identified incorrectly or even omitted altogether, which could have affected my final conclusions. Thus, future research could only benefit from further examinations into the existence of silent and vocal play faces.

4.3 Implications of study

Laughter has been studied for decades yet the amount of empirical evidence for its existence among great apes, let alone humans, is limited. However, the most recent research by Ross (2007), suggests that orangutans can and do produce vocal laughter. In addition, my study found that some orangutans emitted vocalizations while exhibiting play faces, but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfil the definition of laughter used in this study.The orangutans in this study do, however, consistently produce silent play faces in the context of tickling.

4.3.3 Why laughter, as defined by this study, does not exist

Definitively determining whether orangutans produce what we currently regard as laughter would have important implications for the evolution of human communication systems. If my finding is correct and orangutans do not produce high rates of vocalized play faces or laughter as defined by this study, it could be due to the fact that laughter is a social behaviour and orangutans are the least social and the most solitary of all the great apes. On the other hand, I did find significant evidence for the exhibition of silent play faces. This suggests that play faces, or silent laughter, may have evolved prior to the vocalization and offers the possibility that the origin of laughter commenced as a facial expression even farther back in evolutionary history.

Another point to consider is the possibility that the low rates of vocalizations and the high frequency of play faces suggest that the perception of this signal requires greater sensitivity. For instance, Gosselin (1997) states that the perception of anger at low levels is more likely to provide a fitness advantage (In Schmidt and Cohn 2001). From this, it can be hypothesized that orangutans have a greater sensitivity to perceive low-cost silent laughter or play faces over vocal laughter as the latter would be a fitness disadvantage.

A final point to consider here concerns the frequency criteria used to determine the existence of orangutan laughter. Perhaps the expectation that orangutans must exhibit play faces and vocalizations together 50% of the time is too high. In fact, this frequency criteria for human laughter has not yet been determined. Therefore, making comparisons across species is not possible when there is no basis for what constitutes a proper rate of expectation among humans.

4.3.4 Few comparable studies

The second point of discussion is that there is a limited framework or context in which to place the findings of my research. There were no other studies at the time the research was designed and to my knowledge there are still none that test humans, primates, or any of the great apes using the exact methods and analysis that I employed. The implications of this is that it is difficult or impossible to arrive at conclusions about whether or not orangutans behave or laugh like other great apes and humans as a lack of similar qualitative and quantitative analyses limits comparisons.

4.3.5 Definition problems

The third issue stems from the definition of laughter against which the orangutans in this study were judged. It forces one to question whether the definition used in this study was too restrictive and rigid causing the wrong questions to be asked. In an attempt to find laughter, if I set out seeking specific characteristics or criteria outlined by a narrow definition, the findings are going to reflect different results than if the definition was broader and more flexible. This opens the debate as to whether the current definition of laughter is incorrect or not inclusive enough. It also raises the possibility that laughter research needs to consider a larger array of behaviours in addition to vocalizations that so far play a very strong and deterministic role in the identification of laughter.

In terms of its identification, as a muscular or physical phenomenon, laughter is relatively easy to describe. However, the wide range of definitions makes it harder to establish one standard set of characteristics which could be used to label vocal laughter as such. The basic division of laughter into its Duchenne and non-Duchenne components by some researchers has already been outlined. However, to complicate matters, there are also different variations of laughter that may reflect entirely different purposes (Armstrong 1928; Glenn 2003; Pollio et al. 1972; Provine 1996). These variations have been categorized into groupings depending upon the extent, pitch, and tone of the vocalization and the level of intensity providing a whole scale of words used to describe the act of laughing. While the laugh is the general word for the sounds of exhalation made in expressing joy, mirth, and amusement, to chuckle is to laugh quietly in low tones and with mild amusement or satisfaction, especially to oneself. Giggle and titter are half-suppressed laughs often consisting of a series of rapid, high-pitched sounds but whereas the titter may be used to indicate affected politeness, the giggle is usually a light, convulsive laugh in a silly or nervous manner. The snicker is also a half-suppressed laugh but slyly when laughing at another's discomfort or a bawdry story. There is the snort, which is to force air violently and noisily through the nostrils. The chortle, a combination of the chuckle and snort, is to utter with joyful glee, and lastly there is the guffaw used to describe the burst of rude, loud, coarse, and boisterous laughter (see Roeckelein 2002). As a result, it is easy to see how applying the various definitions of human laughter can become further complex when considering this behaviour in other species. In addition, great apes, including the orangutan, have been found to vocalize during play and tickling contexts while inhaling and exhaling, which contradicts the part of the definition of laughter that states it is only during exhalation.

Another point that needs to be addressed is that while in general agreement as to the fundamental physical properties that define and allow for the measurement of human laughter, researchers also tend to disagree on some issues. Bachorowski and Owren (1999) contend that human laughter is predominantly comprised of neutral 'huh-huh' sounds and is less stereotypical. They emphasize its variability, recognize that it can consist of both voiced (tonal) and unvoiced (atonal) elements, and classify laughter into three basic categories: high-pitched, song-like laughs that do fit the stereotyped notions; snort-like laughs with sounds primarily produced through the nose; and grunt-like laughs produced through the mouth. They recognize that there is a rich repertoire of laugh vocalizations with some sounding more like bird chirps, pig snorts, frog croaks, and chimpanzee "pants" rather than normal human utterances. They suggest that their findings support the notion that laughter is merely one part of a larger package of subtle tools used by humans in different contexts depending on the situation and with whom they are interacting.

The implication of the above is that perhaps the definition of laughter needs to be re-examined. There is no one specific definition of laughter that can be applied to all situations, all individuals, all humans, or all primate species. While this study did not find orangutans to emit vocalized play faces when being tickled, it raises the question as to what definition of laughter was being employed and thus, what criteria were being measured, and how did this affect the results? In addition, these definitions strongly emphasize the role of vocalizations in the identification of laughter when explanations of its existence place it within a larger array of behaviours. The importance of the vocalized aspect cannot be denied among humans. However, even among the human species there are individuals who emit, and circumstances (e.g., tickling) that elicit, a silent laugh-like response whereby no vocalization is produced at all. However, the response does include other behaviours — facial expressions (play face or facial laughter) and body language (i.e., biting of hand, curling up to protect tickling zones) that is similar across species under these conditions. In fact, evidence for this was found in the comparable observations between my own young children and the orangutans used in this study. Furthermore, there is a lot of inter-individual variation in both humans and orangutans. Among humans, some individuals do not respond to tickling in a way that meets the criteria for laughter as outlined by this study. On the other hand, some orangutans do respond in a way that meets criteria for laughter as outlined by this study. This does not mean that humans do not laugh and orangutans do. This suggests that the definition of laughter needs to be consistent and able to account for the individual variation in both species.

4.3.6 Silent laughter, social intelligence, and human evolution

While some orangutans in this study did emit vocalizations while exhibiting play faces, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. Therefore, the existence of vocal laughter among orangutans could not be supported. However, this study did provide evidence for what could be considered silent laughter which has strong evolutionary implications in itself. In an attempt to define human culture and social intelligence, much effort has been directed toward the brain. However, social intelligence is also apparent in other adaptations that support positive relationships in social groups. While facial expressions are one form of social behaviour that provide insight into intentions, motivations and emotions of individuals, the study of the face has not been fully explored. In the past, the interpretation of facial expressions and non-verbal communication has mainly been the discipline of psychology or other branches of anthropology. However, in order to investigate social intelligence as a major factor in human evolution, additional research from the perspective of physical anthropology is needed. Therefore, the play face, a social behaviour, and a form of non-verbal communication is an excellent and reasonable source of insight into cognitive and behavioural adaptations.

Schmidt and Cohn (2001) established facial expressions as a potential behavioural adaptation and use the human smile as an example of this evolutionary approach for understanding human facial expressions. Like the smile, laughter serves to increase cooperation and affiliation during social interactions while decreasing the negative effects of others. Because this is also the function of any adaptive signal that has positive fitness consequences (Schmidt et al. 2001), laughter too, can be said to be an adaptive social signal. More specifically, silent laughter is essentially a play face, a facial expression used to send a message to individuals involved in play that the interaction is not serious fighting and is in fact play. As such, the signal of silent laughter among orangutans can provide evidence for the origins of non-verbal communication in humans and must have played an important role in the evolution of social intelligence.

Clearly there are going to be differences in the frequency and intensity of facial expressions across normal individuals in a population (Schmidt et al. 2001). In fact, I found much inter-individual variation in the frequency and duration of facial expressions in the context of tickling; in addition, Ross (2007) states that orangutans displayed the most distinctive laughter among all the great ape species in her study which was also not produced exactly like human laughter or other great apes for that

matter. The implications of these findings suggest that the consideration of non-human primate facial expressions would be specific to each individual species and it has been suggested that while some homology is expected, it is possible that divergent facial signaling systems have evolved (Schmidt et al. 2001). In the case of orangutans, it would not be surprising that this has happened as fossil evidence indicates the human and orangutan lineage separated 10-14 million years ago (Galdikas, 2013).

As was discussed in the introduction of this thesis, some support the view that non-verbal communication represents an ancestral primate while language is uniquely human (Eibl-Eibesfeldt 1989). Human social intelligence is a major factor in the evolution of the human brain and language is our most adaptive system of social signalling (Pinker 1994 In Schimdt et al. 2001). While there is no doubt that language was a driving force in the evolution of human behaviour, there is more to social intelligence than language (Schmidt et al. 2001). Attention needs to shift toward the evolution of non-verbal communication systems, including facial expressions like silent laughter, and from various perspectives especially that of physical anthropology.

4.4 Future research

In the first part of this chapter, alternative options to the methodologies employed in this research were discussed. Those that were considered and subsequently rejected had their strengths and weaknesses but due to time, money, feasibility, and caregiver availability, could not be applied to this study. In the end, methods used in the field and during the analysis stages were chosen as they met the needs of this study most effectively. However, they do leave room for further examination. In fact, if further studies are to investigate the existence of laughter in orangutans or other great apes, there are a few areas that require further consideration. In this section I discuss four major issues that would benefit from work in the future: the need for properly controlled studies on humans and additional ape species; laughter's existence in other contexts such as natural social play; the need for a reconsideration or expansion of the definition; and investigations into the relationship between facial expressions and vocalizations.

The first major deficiency in laughter research thus far is the lack of properly controlled studies. Further investigations are required with additional great ape species (gorillas, bonobos, orangutans) of different age groups and from various locations, other primates (i.e., gibbons) with different mating systems or social dynamics, for example, and of course, humans, especially children of all ages and cultures. This

needs to be accomplished in order to arrive at a general framework so that further ethological studies have something to which they can compare their results. As it currently stands, this does not exist. In addition, prior psychological studies have generally taken a cross-sectional approach, measuring a few minutes of expression in a large number of individuals (Schmidt and Cohn 2001). Since longitudinal studies of facial expressions are small (see review in Messinger et al. 1999 In Schmidt and Cohn 2001), this is one area in which laughter origins should focus.

The second major deficiency in laughter research is that future studies need to examine the possible existence not only in other species but also in additional contexts. Perhaps tickling does not present the best conditions under which to elicit these vocalizations and facial expressions. In fact, it is highly likely that given the time, money, and accessibility, testing the hypothesis that laughter exists among orangutans would be best studied under natural play conditions when subjects are instigating play behaviour with con-specifics whether this is in rehabilitation centres or zoo environments in different locations around the world.

Some researchers (e.g., Ross 2007) have acknowledged that, like humans, orangutans produce more than one type of vocalization in association with play faces. Therefore, the third major requirement for future research is that the definition of laughter needs to be reconsidered, expanded, or amended. As a result of, or more appropriately, as part of this re-defining process, the physical properties of laughter need to be identified. This would allow future studies to reapply these characteristics to other species — humans, great apes, or otherwise — where comparable data is lacking and extremely necessary.

The fourth and final issue to be discussed in this section pertains to the need for future examination of play faces, vocalizations, and the relationship between the two. Initially, further research should examine the presence and function of the different play faces during different play contexts among humans and the great apes. According to Van Hooff and Preuschoft (2003), humans and bonobos habitually employ the open-mouth bared teeth (OMBT) version whereas chimpanzees, gorillas, and siamangs produce the classic relaxed open mouth (ROM) display. My study discovered that orangutans also exhibit the former significantly more often that the other play faces, but the situation for orangutans and gibbons is poorly documented (Chevalier-Skolnikoff 1982; Preuschoft & Van Hooff 1997). As such, the role and function of the various play faces needs to be investigated and placed into the larger framework of this behaviour.

As just discussed, perhaps the current definition of laughter places too much emphasis on the vocalized aspect of laughter due to its important role among humans. However, on the other side, further examination is needed into the vocalizations themselves. Very few studies have focused on play panting in primates and perhaps the low amplitude of the vocalizations makes it difficult to conduct detailed analyses on play panting in most of the primate species. Regardless, this definitely needs to be addressed in order to obtain a better understanding of what laughter looks like. This process could also involve examining which sounds appear with which play faces, what are their properties, what do they sound like among different species, and ultimately asking what laughter looks and sounds like among orangutans and other great ape species.

This leads to the final area where future research is required. The various play faces, including if, how, and when they co-occur with vocalizations, is a major issue worthy of further exploration. This is due to the fact that their relationship is what currently defines laughter in humans. As previously discussed, some species produce play panting in association with the ROM while other species in association with the OMBT display. As well, the same species sometimes produce play panting in association with both depending on the situation. Specifically, Van Hooff found that although chimpanzees often emitted play pants with the OMBT, he discovered that they also sometimes vocalize with the mouth only slightly open which is apparently different from the typical play face that occurs in a playful encounter. Thus, there seems to be a difference in the context of occurrence between play panting and play face among chimpanzees. In social play interactions, mainly the targets of 'aggressive' actions produce play panting and that this play panting rarely exists prior to the initiation of play. However, it has been reported that chimpanzees often present play faces in both of these situations — before they mouth their targets (Plooij 1979) and to initiate play (Hayaki 1985). Van Hooff (1972) stated that this could be regarded as an intentional movement of mouthing and similarly to Plooij (1979) called it a "ready to bite face." Therefore, it is plausible to assume that play panting and play faces contain different motivational states and may have unique roles in social play interactions among chimpanzees and other species as well.

During the initial stages of my study on orangutans, I had started to examine the relationship between specific vocalizations and the four different play faces. Due to a lack of time and inexperience in this type of analysis, it was recently omitted from this study. Although it would have been an extremely beneficial and insightful extension to my research, the reduction and summary of vocalizations into ten subjective

categories as I had done was problematic for a number of reasons. Because I am a novice vocal analyst, it is possible and very probable that these vocalizations were not identified accurately, that some were omitted from the study, or that they could have been categorized differently. Although I had attempted to utilize schemes previously developed by other researchers (e.g., Ross 2007), my study was not based on acoustic spectrographic analysis, hence causing my categories to be even more subjective. In light of all this, investigating the relationship between play faces and vocalizations is probably the single, most critical piece of evidence missing from the current body of research. Overall, the body of knowledge and evidence on laughter is limited and there is a large gap in its phylogeny and evolutionary history. Thus, in order to gain a more comprehensive understanding of laughter in the future, it is imperative that we acquire further empirical data on the presence and function of silent and vocal play faces in a larger number of subjects, species, and contexts.

Chapter 5
Conclusion

Laughter is a ubiquitous human phenomenon and while its existence has been relatively well established in chimpanzees, very few studies have investigated beyond this species. The most common theory is that human laughter evolved from facial expressions associated with great ape play and tickling and as only one other study had been undertaken on orangutans thus far, they seemed like a reasonable and necessary place to search.

Previous research implies that the study of laughter may exist outside of humans but the majority of research has primarily focused on chimpanzees. In fact, the evidence of laughter in other great ape species is scarce (e.g., Andrew 1963; Marler & Tenaza 1977; Matsuzawa 2001; Palagi 2007; Peterson 2001; Provine and Bard 2000; Ruch et al. 2001; Van Hooff 1972, 1976; Van Hooff et al. 2003; Waller & Dunbar 2005) and mainly consists of the occasional anecdote from field observations (e.g., Darwin 1872; Fossey 1972; Marler and Tenaza 1977; Maple 1980, 1982; Van Lawick-Goodall 1971). There has been only one other study on orangutan laughter (Ross 2007) and it suggested that laughter exists among this species as well. As a result, the orangutan became a logical and necessary place in which to search for further evidence of laughter behaviour.

This study found that while some orangutans emitted vocalizations with play faces when tickled, the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfil the definition of laughter used in this study.. However, they did often produce play faces in response to tickling. These responses do not appear to be influenced by sex, age, or time spent in rehabilitation. The following chapter is going to summarize these findings, placing them in relation to the four hypotheses outlined in chapter one, and will conclude by re-emphasizing the contribution this study makes to the understanding of the evolutionary history of laughter.

5.1 Hypothesis #1: All subjects

Based on previous research (e.g., Ross 2007) that states orangutans emit vocalizations when producing play faces, this study first examined the presence and frequency of both play faces and vocalizations among orangutans when tickled. I predicted that if the hypothesis is supported then orangutans will produce both silent and vocalized play faces more frequently than non-play faces when the full sample of orangutans is considered.

When investigating the presence and frequency of play faces, the current study found that 70% of the time play faces occurred more often than non-play faces. Specifically, it was found that out of the four possible play faces, 77% of the occurrences were PF 3. This means that when orangutans produce a play face, they are most likely to do so with an open-mouth bared teeth display. Both of these findings were statistically significant. Furthermore, the silent play face made up 75% of the play face displays versus 25% that were vocalized play faces. Because vocalizations and play faces co-occur at rates lower than the criterion needed to meet the definition of laughter as outlined in this study, orangutans do not appear to laugh. Conversely, orangutans do produce play faces 75% of the time.

5.2 Hypothesis #2: Sex

As discussed earlier in this thesis, the motor-training hypothesis of play put forth by Maestripeir and Ross (2004), argues that male infants exhibit higher frequencies of social play than female infants. Accepting tickling as one aspect of social play, and if males play more than females, then one should expect a higher frequency of play vocalizations among male orangutans as well. Thus, in this section of the study, I tested the hypothesis that there are sex differences in the presence and frequency of both play faces and vocalizations among orangutans in the context of tickling. I predicted that if this hypothesis is supported, than both silent and vocalized play faces would occur more frequently among male orangutans than among females.

When investigating the sex differences in the frequency of play faces, the current study found that overall play faces were more common than non-play faces for both sexes. Of the total male responses, 75% were play faces and for the females 64% were play faces. However, this finding was not statistically significant so the hypothesis was not supported: neither males nor females exhibit a play face more often than the other sex.

Silent play faces were much more common than the vocalized for both sexes. Overall though, males made up 63% of the total silent play faces, 59% of the total vocal play faces, and 62% of the total play face responses. However, these results were not statistically significant so it was concluded that the hypothesis was not supported: males do not produce a play face or play vocalization more than female orangutans.

5.3 Hypothesis #3: Age

In this section of the study, I tested the hypothesis that age affects the presence and frequency of play faces and vocalizations in infant orangutans when tickled. I predicted that if this hypothesis is supported than older orangutans will produce play faces and play vocalizations more frequently than the younger orangutans.

When examining the presence and frequency of play faces, this study found that age did not alter the finding that play faces were more common than non-play faces. This was especially so for age group 2 (25-36 months) who produced the most play faces by the most individuals and in the highest numbers. However, when comparing the percentage of play faces overall, for age groups 1, 2, and 3, play faces made up 64%, 72%, and 77%, respectively, out of the total number of responses for each group. While these results initially indicate that the production of play faces increases with age, the findings were not statistically significant, so the hypothesis is not supported: no age group produces play faces significantly more frequently than the others.

Also, age did not alter the finding that the PF 3 was much more common than the other play faces, making up 77% of all play faces when all groups were considered. For age groups 1, 2, and 3, the PF 3 was exhibited 64%, 81%, and 85% respectively out of all the other play faces in each group, with group 2 producing 59% of the total PF 3 out of all groups. So again, while there appears to be an initial indication that the production of OMBT displays increases with age, this discovery was not statistically significant. As such, the hypothesis was not supported: no age group produces OMBT displays more frequently than the other age groups.

This study found that orangutans from all age groups emitted vocalizations while exhibiting play faces but the rate at which the two behaviours co-occurred in the sample was lower than the level required to fulfill the definition of laughter used in this study. Silent play faces made up 76-85% of the total play faces for each group and

were 2.5–6 times higher than the vocal play face responses. It was also discovered that age group 2 produced 53% of the total silent play faces, 63% of the total vocal play faces, and 56% of all play faces. However, analysis found none of these findings to be statistically significant so the hypothesis was not supported: age does not affect the production and frequency of silent and vocalized play faces. Thus, the existence of laughter could not be supported by this study.

5.4 Hypothesis #4: Time spent in rehabilitation

In this section of the study, I tested the hypothesis that the length of time an orangutan has spent in rehabilitation at the Care Centre affects the presence and frequency of play faces and vocalizations among orangutans when tickled. I predicted that if this hypothesis is supported, silent and vocalized play faces would occur more frequently among those orangutans who had lived at the OQCC for a greater period of time.

When examining the presence and frequency of play faces, this study found that time in rehabilitation did not alter the finding that play faces were more common than non-play faces. In fact, play faces made up 91% of group 1 responses, 67% of group 2 responses, and 55% of group 3 responses. Therefore, it initially appeared that time at the Care Centre decreased the production of play faces. However, these findings were not statistically significant so the hypothesis was not supported: no group exhibits a play face significantly more than the other groups; therefore, time in rehabilitation does not affect the presence and frequency of play face production among orangutans.

Controlling for time spent in rehabilitation, also did not alter the finding that the PF 3 was much more common than the other play faces. For all time groups, the PF 3 made up between 73-77% of the total number of play faces, with group 2 making up 73% of this total, group 1 only 22%, and group 3 with only 5% of the PF 3 displays. Descriptively there were no obvious patterns and this was confirmed statistically. Therefore, the hypothesis was not supported: no time group exhibits an OMBT display more than the others so time in rehabilitation does not influence play face production.

All three groups exhibited silent play faces in much greater frequency than vocalized play faces, with the former making up 68–89% of the total number of play faces. In addition, it was group 2, whose subjects had been at the care centre between 13 and 24 months that produced the highest results making up 73% of all PF responses, 69% of the total silent play faces, and 84% of the vocalized play faces. So

overall, it appears that vocalized play faces or laughter as defined by this study, occurs less frequently than vocalizations with non-play faces. This finding is not affected by the amount of time an orangutan has spent at the Care Centre. These findings were once again not statistically significant so the hypothesis was not supported: no time group produces a vocalized play face more than the others. In terms of silent play faces, while they occurred predominantly more often that the vocalized play faces, statistically these results were not significant so it was also concluded that time in rehabilitation does not affect the production and frequency of either silent or vocalized play faces.

5.5 Conclusion

When investigating the existence of laughter among orangutans, this study found that play faces occur more frequently than non-play faces, and that when orangutans do produce a play face, they indicate a preference for the silent OMBT display. These findings were statistically significant. In addition, silent play faces occur more frequently than vocalized play faces. In the end, it was concluded that some orangutans emitted vocalizations when producing a play face but it was not at a rate high enough to meet the definition of laughter as outlined by this study. However, they consistently produce silent play faces using an OMBT display. While these results remained throughout the study they were not statistically significant for the other three hypotheses. Therefore, it was determined that sex, age, and time spent in rehabilitation at the Care Centre do not appear to affect the production and frequency of either silent or vocalized play faces among orangutans when tickled. Thus, the analyses do not support the existence of laughter as defined by this study.

It is important to note that while statistically, vocalized play faces, or laughter as defined by this study, were not found, there were instances in this study in which laugh-like emissions were heard. The sounds produced by orangutans during these tickling episodes correspond to sounds emitted by humans. However, it is difficult to categorize them as such without conducting spectrographic analysis and based on the broad definition of laughter that is currently known. As it has already been recognized that the definition of laughter is problematic, it is one issue that must definitely be addressed before further conclusions can be made on the existence or non-existence of laughter among other species.

While this study found that orangutans do not vocalize at high rates when producing a play face, the fact that they produce all play face variants during tickling,

suggests that orangutans can be said to laugh facially or silently. According to Van Hooff and Preuschoft (2003), the ROM is ancestral to OMBT but little is really known about the differences between these displays in species other than the chimp and bonobos. They may occur side by side or may serve different functions. Among the orangutans, the OMBT display was significantly more common than the other play faces, however the others were observed in this context as well. Therefore, this is one aspect that requires further investigation as the specific function of facial displays in primates is poorly understood, even despite the widespread acknowledgement of the likely importance of facial communication (Waller & Dunbar 2005).

As previously mentioned, human laughter is argued to have started with the silent form or play face variants in the context of play and tickling. As well, it has been suggested that play contributes to individual survival and reproductive success (Fry 2005) at both the level of the individual and the species in which it is found. Thus, the associated play signals, like vocalizations and play faces, discovered among orangutans can provide significant insight into innovation, social affiliation, dominance hierarchies, communication, cultural transfer, cognitive capacities, and positive emotional experiences (Lewis 2005).

While evidence for high rates of vocalized play faces was not found, this study indicates that the silent OMBT play face is used among orangutans in the context of tickling. But this study also confirms that in order to fill in the missing gaps, we need to investigate the role and function of various play faces and vocalizations, in a number of different species and contexts over time. As defined by this study, the existence of laughter among orangutans could not be statistically supported. However, play vocalizations co-occurring with play faces have been observed in orangutans. Furthermore, this study concludes that silent play faces do exist among orangutans, regardless of sex, age, and time in rehabilitation, suggesting that a form of laughter is part of the play communication system among orangutans. As such, they are one species that could provide important insight into the origins of human laughter, communication, and ultimately, human culture.

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