

**A white-cheeked crested
gibbon ethogram**

&

A comparison between siamang (*Symphalangus
syndactylus*) and white-cheeked crested gibbon
(*Nomascus leucogenys*)

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Juli – November 2004

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Final project Animal management

Projectnumber: 344311

Juli 2004 – November 2004-12-01

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Keywords: White-cheeked crested gibbon (*Nomascus leucogenys*), Siamang (*Symphalangus syndactylus*), ethogram, behaviour elements.

Preface

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Leeuwarden, November 2004

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Summary

Gibbons form the family Hylobatidae and are often referred to as the “small apes”. They are distributed throughout the tropical rain forests of South-East Asia. Currently, four distinct genera of gibbons are being recognised, including *Hylobates* (lar-group), *Bunopithecus* (hoolocks), *Nomascus* (concolor-group or crested gibbons), and *Symphalangus* (siamangs). Recent studies challenge the notion that gibbons are a uniform group and suggest that ‘the’ typical gibbon does not exist. Using one gibbon taxon to represent all gibbons in a study may bias the results. So far, a reliable and comprehensive ethogram for gibbons has been published for only one gibbon taxon, the siamang, (Orgeldinger, 1999). A comparison between the siamang ethogram and an unpublished white-cheeked crested gibbon ethogram (Hold, 1998) is limited by the small sample size of the latter (four family groups). Therefore, one goal of this study consisted in collecting supplementary ethogram data for a fifth group of white-cheeked crested gibbon, in order to make the ethogram more representative and in order to facilitate a comparison with the siamang ethogram.

A family of three white-cheeked crested gibbons (*Nomascus leucogenys*), housed on an island in Apenheul Zoo (Apeldoorn), was observed for 84 hours over a two week period. The group included an adult pair and their male infant of an age of 15 months. Behavioural data were collected using the same method as in an earlier study on white-cheeked crested gibbons (Hold, 1998), in order to make the data comparable. Focal animal sampling was used to record the frequencies of each behavioural element, and scan sampling was applied to record the inter-individual distances within the group.

As a result of this study, nine behavioural elements have been added to the earlier ethogram of Hold (1998). An ethogram will never be complete, but the combined ethograms of this study and Hold (1998) should be seen as a starting point, intended to stimulate and assist further studies of white-cheeked crested gibbon behaviour.

This study shows that only two behaviour patterns are exclusively performed by the gibbon group of Apeldoorn. The adult female of this group exhibited ‘jerky body movements’ (70 times during 28 observation hours), and both the male and the infant performed, the behaviour ‘sliding down rope/tree-trunk’ (2 and 4 times, respectively). Both the male and the infant of this group were significantly more active than the female. The infant was playing most of the time with the male, and it was being groomed most often by the female. The mother-infant bond appears to be very strong in every white-cheeked crested gibbon group studied so far. Mother and infant spent more than 80% of the observation time within a distance of less than three meters away from each other. The female was not only nursing the infant, but she also exclusively shared food with the infant, and carried the infant.

A comparison between the ethograms reveals that the behavioural elements of the siamang and the white-cheeked crested gibbon are fundamentally similar. The siamang ethogram is, however, far more comprehensive (190 behavioural patterns) than the white-cheeked crested gibbon ethogram (83 behavioural elements). For instance, behavioural elements like ‘facial expressions’ are mentioned in the siamang ethogram but are not represented in the white-cheeked crested gibbon ethogram. Possible reasons for this finding may include a difference in the keeping conditions. Whereas all studied crested gibbon groups were kept on islands, the siamang study also included several groups kept in cages. The observer usually can observe caged groups from a closer distance and may be more likely to observe subtle social communication signals.

1. Introduction

1.1 Gibbon Ethograms

Gibbons (Hylobatidae) are monogamous arboreal apes living in East Asian rainforest. Family groups, usually two to five animals, typically consist of an adult pair and their immature offspring (Chivers 1977, 1989; Geissmann, 2003; Leighton 1987). Gibbons are prototypical brachiators, with long arms and hands and flexible forelimb joints. Gibbons have been regarded as a very uniform group of primates in the past. They all appeared to share the same social structure, the same anatomic specialisations, the same ecology, etc. As a result, many studies on apes usually include up to three genera of great apes, and only one sample of the gibbons. More recent research show that gibbons are a less uniform group than believed previously. For instance, the analyses of DNA sequences by Roos and Geissmann (2001) revealed that 4 distinct genera of gibbons should be recognised, namely: *Hylobates* (*lar*-group); *Bunopithecus*; *Nomascus* (*concolor* group) and *Symphalangus* (siamang). These genera are at least as distantly related as *Homo* and *Pan*. The white-cheeked crested gibbon is a species of the genus *Nomascus*. Crested gibbons occur in tropical evergreen and less seasonal parts of semi-evergreen rainforest of Indochina (i.e. southern China, Vietnam, Laos and Cambodia). Analyses of calls revealed that gibbon songs appear to follow different strategies and fulfil different functions, depending on species (Geissmann et al., in press, Geissmann and Orgeldinger, 2000). Finally, as yet unpublished data by Geissmann et al. (in prep.) indicate that the monogamous social structure in gibbons may be under different regulation in different taxa. These studies challenge the notion that gibbons are a uniform group and suggest that ‘the’ typical gibbon does not exist. Using one gibbon taxon to represent all gibbons in a study may bias the results in a similar way as using only one great ape taxon to represent all great apes.

A good ethogram is the working basis for behavioural research. An ethogram is a catalogue of descriptions of the discrete, species-typical behaviour patterns that form the basic behavioural repertoire of the species (Lehner, 1987). In most cases, it is desirable to create an ethogram in which the categories of behaviour are objective, discrete, and do not overlap with each other. Definitions should be clear, detailed and distinguishable from each other. Ethograms can be as specific or general as the study warrants. Alternatively, some studies seek to describe all facets of a particular animal's behaviour, and the appropriate ethogram will comprehensively categorize any and all behaviours that may occur.

A reliable and comprehensive ethogram for gibbons has, so far, been published of only one gibbon taxon, the siamang (Orgeldinger, 1999). Whether this ethogram can be applied to other gibbon species and genera is questionable, especially considering the generally underestimated diversity of gibbons, as discussed above. Therefore, an equally comprehensive and reliable ethogram for a second taxon will enable to make a first assessment of the behavioural diversity of gibbons. An ethogram comparison between two different gibbon taxa can show if the behaviour of each genus corresponds with each other or if the behaviour differs from one another.

A relatively comprehensive ethogram has been published for the white-handed gibbon (*Hylobates lar*) by Baldwin and Teleki (1976). Unfortunately, the white-handed gibbon ethogram is flawed for several reasons:

- 1) Representativity of the ethogram of *H. lar* may be limited. The study animals were kept as peer groups of mostly juvenile individuals and not in family groups (the typical social unit in wild gibbons).

- 2) During the study on *H. lar*, the study animals were also used for electrophysiological experiments (Delgado et al., 1978). This can influence the behaviour, the animal can show stress related and/or apathetic behaviour and less natural behaviour.
- 3) Purely qualitative data was collected on *H. lar*, whereas on *S. syndactylus* both qualitative and quantitative data were collected.

These flaws in the published ethogram for *H. lar* limit its comparability with other ethograms.

For this research a comparison is made between 1) the behaviour of a male and female of a white-cheeked crested gibbon group, 2) the behaviour of two different age classes (adult and infant) of a white-cheeked crested gibbon group and 3) a comparison between a white-cheeked crested gibbon ethogram and a siamang ethogram.

An unpublished ethogram of white-cheeked crested gibbons (*Nomascus leucogenys*) (Hold, 1998) was collected with the same methodology as the one used in the siamang study by Orgeldinger (1989, 1999). A comparison approach between the white-cheeked crested gibbons (Hold, 1998) and the siamang (Orgeldinger, 1999) ethogram is limited only by sample size. Whereas the siamang data cover 12-14 groups (depending on variables), crested gibbon data are available for only four groups. Therefore, collecting data on a fifth gibbon family group would improve the sample and the relevance of a comparison with the published siamang ethogram. For collecting data on the fifth gibbon group, a family white-cheeked crested gibbon group (including an adult pair with their infant) has been observed in Apenheul (Apeldoorn) with the same methodology as used by Hold. Apenheul is a zoo in the Netherlands which is specialised in apes and monkeys. The gibbons observed by both Hold (white-cheeked crested gibbons) and Orgeldinger (siamang) were kept in family groups in various zoos. Both studies used the observation method *focal animal sampling* for collecting data. Hold observed an individual animal on average for 29 hours and Orgeldinger observed an individual animal for 40 hours. *Scan sampling* has been applied to record the spatial division of an individual in a group (individual distances) divided over a day. The measuring of spatial division of an individual in a group makes it possible to explain the group cohesion (Chivers, 1971; Palombit, 1992) and the probability of social interactions (Palombit, 1992). The white-cheeked crested gibbon ethogram of Hold (1998) is illustrated with photos of various behaviour elements, but short video clips are not yet available.

1.2 Goal

One goal of this report is to serve as a representative ethogram for behavioural studies on white-cheeked crested gibbons, both in written form and – in representative – in the form of short video clips to be made available to the research community on the internet.

The second goal of this study is to provide a detailed behavioural comparison between male and female, adult and infant and a comparison between white-cheeked crested gibbons and siamang.

1.3 Research Questions

- 1) Is the ethogram of white-cheeked crested gibbons (Hold, 1998) complete and representative, or are there any behavioural elements that should be mentioned, but are missing in this ethogram? If so, which ones?
 - a. Does the gibbon group in Apenheul show any typical behaviour that only occurs in this specific gibbon group and has not been observed in the four gibbon groups observed by Hold (1998) and is not mentioned in the ethograms

for siamangs (Orgeldinger, 1999) and white-handed gibbons (Baldwin and Teleki, 1976)? If so, which behaviours are these?

- b. Are there any behavioural elements exclusively shown by the four groups of white-cheeked crested gibbons observed by Hold (1998) and has not been seen in Apeldoorn? If so, which behavioural elements are these?
- 2) Do the individual distance classes of the white-cheeked crested gibbon group at Apenheul correspond with the individual distance classes of the 4 white-cheeked crested gibbon groups studied by Hold (1998)?
- 3) Are there any differences between the behaviour of males and females?
- 4) Are there any behavioural elements that only occur within certain age-classes (adult or infant)? If so, which ones.
- 5) Do the ethograms of white-cheeked crested gibbons and siamang gibbons differ? If so, what is/are the difference(s)? Are any behavioural elements exclusive to either white-cheeked crested gibbons or siamangs?

For research questions (1), (2) and (5) the data of this study are combined with the data on four different groups of white-cheeked crested gibbons previously collected by Hold (1998). For research questions (3) and (4) only the data of this research is being used. For the research question (5), the combined data for white-cheeked crested gibbons are compared with siamang data collected by Orgeldinger (1989, 1999).

This report contains 5 chapters. The first chapter provides information about the problem description, goals and research questions of this study and general information about gibbons, in particular the white-cheeked crested gibbon (*Nomascus leucogenys*) and the siamang gibbon (*Symphalangus syndactylus*). Chapter two describes the materials and methods used during this study. The following two chapters contain respectively the results (chapter 3) and the discussion (chapter 4). The final chapter covers the conclusion.

1.4 Gibbons

The gibbons form the family *Hylobatidae* and are often referred to as the “small apes” [The term “lesser apes” should not be used anymore because it has a derogative meaning]. Gibbons form a relatively homogeneous group of species which are distributed throughout the tropical rain forests of South-East Asia (Chivers, 1977; Geissmann, 1995b, 2003; Groves, 1972; Marshall & Surgardjito, 1986). They are unusual among primates in several respects which can be summarised under three key complexes: locomotion, social structure, and communication.

Locomotion

Gibbons are characterized by their spectacular arm-swinging form of locomotion (brachiation). They are prototypical brachiators with long arms and hands and flexible forelimb joints. Brachiation is to move from branch to branch with one arm going in front of the other (Napier and Napier, 1985). When they brachiate, they use four fingers of their hands like a hook (but not the thumb). While brachiating a gibbon is able to change direction, even during fastest bounding, by slightly touching a branch. Brachiating constitutes 90 % of arboreal locomotion. Other patterns include climbing, bipedal walking on branches (with or without support of arms).

Social Structure

Gibbons live in monogamous, territorial family groups (Brockelman & Srikosamatara, 1984; Chivers, 1984b; Leighton, 1987). Family groups, usually two to five animals, typically consist of an adult pair and their immature offspring (Chivers, 1977, 1989; Leighton, 1987).

Communication

All gibbon species produce long and loud song bouts which are typically produced in the early morning. In most species, mates combine their repertoire in relatively rigid, precisely timed and complex vocal interactions to produce well patterned duet songs (e.g. Marshall & Marshall, 1976; Haimoff, 1983, 1984; Geissmann, 1993, 1995b). The songs are species specific and sex-specific and can be heard clearly at a distance of up to 1 km. Several functions have been attributed to gibbon songs, most of which emphasise a role in territorial advertisement, mate attraction and maintenance of pair and family bonds (Geissmann, 1999; Haimoff, 1984a; Leighton, 1987).

Systematics

In early studies on gibbon systematics, the Hylobatidae were grouped into two distinct genera including the siamang (*Symphalangus*) on one hand, and all the remaining gibbons (*Hylobates*) on the other (e.g. Napier & Napier, 1967, Schultz, 1933, Simonetta, 1957). It is generally accepted now that the family Hylobatidae can be divided into four systematic groups (*Hylobates*, *Bunopithecus*, *Nomascus* and *Symphalangus*) (e.g. Geissmann, 1995a, 2002b, 2003; Geissmann et al., 2000; Marshall and Sugardjito, 1986; Prouty et al., 1983). Recent DNA sequence data suggests that the four groups should be recognised as full genera (Brandon-Jones et al., 2004; Roos & Geissmann, 2001). This view is summarized in Table 1.

Table 1. Classification of the Hylobatidae (Geissmann, 2002b, Geissmann et al., 2000)

Genus	Species		No. of chromosomes
	Scientific name	English name	
<i>Hylobates</i> (lar-group)	<i>H. agilis</i>	Agile gibbon	44
	<i>H. klossii</i>	Kloss's gibbon	
	<i>H. lar</i>	Lar or White-handed gibbon	
	<i>H. moloch</i>	Javan or Silvery gibbon	
	<i>H. muelleri</i>	Gray, Bornean, or Müller's gibbon	
	<i>H. pileatus</i>	Pileated gibbon	
<i>Bunopithecus</i>	<i>B. hoolock</i>	Hoolock or White-browed gibbon	38
<i>Nomascus</i> (concolor-group, crested gibbons)	<i>N. concolor</i>	Western black crested gibbon	52
	<i>N. sp. cf. nasutus</i>	Eastern black crested gibbon	
	<i>N. gabriellae</i>	Yellow-cheeked crested gibbon	
	<i>N. leucogenys</i>	White-cheeked crested gibbon	
<i>Symphalangus</i>	<i>S. syndactylus</i>	Siamang	50

The gibbon species are often separated from each other by seas and rivers, except for the much larger siamang, which is sympatric with the Lar gibbon in peninsular Malaysia and with the Agile gibbon in Sumatra. Figure 1 shows the distribution of the four gibbon genera (*Bunopithecus*; *Hylobates*; *Nomascus* and *Symphalangus*).

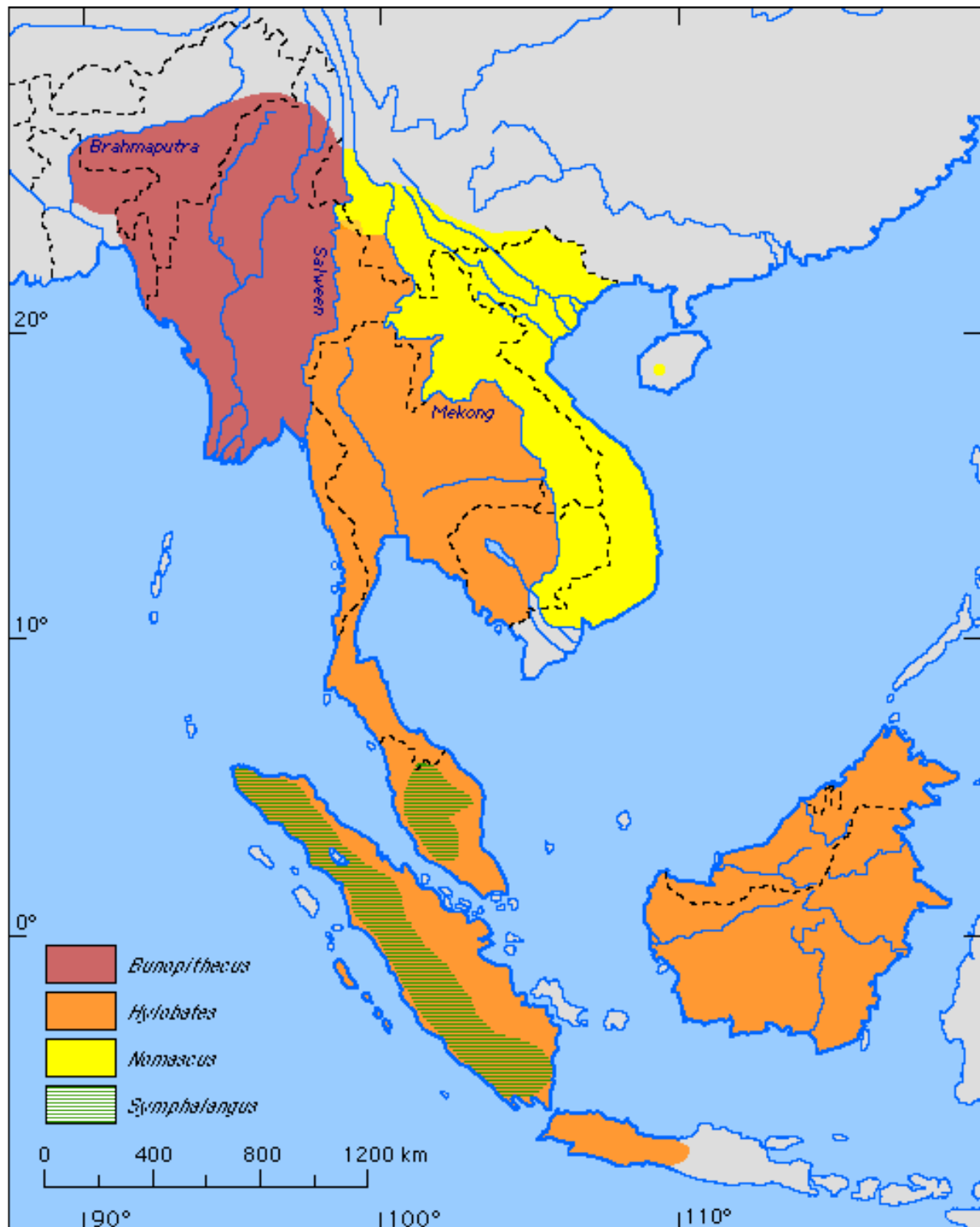


Figure 1. Distribution of the gibbon genera: *Bunopithecus*; *Hylobates*; *Nomascus* and *Symphalangus* (from Geissmann, 1995b, 2003).

1.5 Crested Gibbons (*Nomascus*)

Traditionally, the crested gibbons have been regarded as a single species, *Hylobates concolor* (e.g. Groves, 1972; Marshal & Surgardjito, 1986), but more recent studies suggest that this group should be split into several distinct species (Geissmann, 1997; Geissmann et al., 2000). The most widely accepted and best-described *Nomascus* species are *N. concolor*, *N.*

leucogenys and *N. gabriellae* (western black-crested gibbon, white-cheeked crested gibbon, and yellow-cheeked crested gibbon, respectively). A suggested species-level differentiation between these three species is supported by the fact that all three forms differ markedly in their songs (Geissmann, 1993; Geissmann et al., 2000).

Crested gibbons occur in tropical evergreen and less seasonal parts of semi-evergreen rain forests of Indochina (i.e. southern China, Vietnam, Laos and Cambodia) (Geissmann et al., 2000). Northern white-cheeked crested gibbons (*N. leucogenys leucogenys*) live in the lowland of north-eastern Vietnam and Northern Laos in a subtropical climate with a short and not very cold winter without frost, at elevations of 200-600 m (Dao Van Tien, 1983). Southern white-cheeked gibbons (*N. leucogenys siki*) live in the lowlands at elevation of 30-100 m, in a typical tropical climate, with no influence of the N.E. monsoon and no conspicuous dry season (Dao Van Tien, 1983). Crested gibbons are like all gibbons diurnal, arboreal (going down on the ground very rarely), and are mainly frugivorous (e.g. Leighton, 1987).

Crested gibbons are characterised by various morphological and anatomical features. For instance, the crested gibbons are intermediate in body weight between the large siamang (*Symphalangus*) and the small gibbons of the genus *Hylobates* (Geissmann, 1993). The name crested “gibbons” refers to the erect and elongated crown hair of adult males (Geissmann, 1995a). The male is usually black with or without light cheeked patches, and the female has a lighter colour (light yellow, orange yellow or light beige) and usually has a black cap which is contrasting sharply with the surrounding lighter fur. The crown fur (including the cap) of the female stands straight up, but is not elongated into a crest.

Crested gibbons, as with all other members of the *Hylobatidae*, appear to be dominantly monogamous. A gibbon group typically includes an adult pair and their immature offspring. The average group size ranges from 3 to 5 individuals (Leighton, 1987). Several reports mention larger group sizes for crested gibbons, but these numbers should be regarded with caution. Most likely these larger groups consist of two separate family groups which have encountered each other on the border of their territory. A mated pair produces an average of five to six offspring over a reproductive lifetime of 10 to 20 years (Carpenter, 1940; Tilson, 1981).

Infants are born with a light natal coat, somewhat similar in colouration to that of the adult female. During the first year of life (Delacour, 1934), at the age of about one year (Groves, 1972), or during the second year of life (Dittrich, 1979), the infants change colouration and assume a dark coat which is virtually identical to that of an adult male. At about the time of sexual maturity (at around 5-8 years of age), females change colouration a second time and adopt the light coloration typical of adult females (Delacour, 1934, 1942; Geissmann, 1993, 2003; Groves, 1972; McCann, 1933; Peart, 1935). Young gibbons will stay with their parents until they are past adolescence, then they usually leave the parental groups (Geissmann, 2003; Leighton, 1987).

In terms of singing behaviour, crested gibbons exhibit a number of unique characteristics that set them apart from the other gibbon taxon. According to Geissmann (2002a), the genus *Nomascus* exhibits the highest degree of sex-specificity in its songs, as “there is no overlap between the sexes in note repertoire and no overlap in the phrase repertoire. Female song contributions consist of great-calls only which consist of female-specific notes, whereas males produce short phrases only, and these consist of male specific notes”. Gibbon song bouts are typically produced in the early morning and include sex en species specific characteristics (Geissmann, 1993, 1995b, 2000b, 2002a; Haimoff, 1984a; Marshal & Sugardjito, 1986). Gibbon songs are believed to serve a variety of functions, including defence of resources (e.g. territory, mate), mate attraction, strengthening of pair bonds and advertisement of pair bonds, and these different functions may be exploited by either sex and by different gibbon species (e.g. Cowlishaw, 1992, 1996; Geissmann, 1999; Geissmann & Orgeldinger, 2000; Mitani, 1990; Raemakers & Raemakers, 1985).

1.6 Siamangs (*Symphalangus*)

The siamang gibbon (*Symphalangus syndactylus*) is distributed mainly over the mountain regions of Sumatra and southern peninsular Malaysia (Chivers, 1977; Geissmann, 1995b; Groves, 1972; Marshall & Sugardjito, 1986). The siamang is exceptional among gibbons in that its area of distribution almost completely overlaps those of other gibbons, namely those of the white-handed gibbon (*H. lar*) and the agile gibbon (*H. agilis*) of the *lar* group (Chivers, 1971, 1972, 1974, 1977a; Chivers and Gittins, 1987; Groves, 1972; Khan, 1970; Liat, 1969; Marshall and Sugardjito, 1986; Wilson and Wilson, 1977). Like most other gibbon species, the siamang lives in tropical forest, shows extreme adaptations for arboreal locomotion, a monogamous social structure, and exclusive use of actively defended territories by small family groups (e.g. Chivers, 1974; Chivers and Raemakers, 1980; Norikoshi, 1986; Palombit, 1992; West, 1982). The siamang has almost twice the body weight of the other gibbons (e.g. Jungers, 1984; Schultz, 1973). Siamang home ranges are smaller than those of sympatric *lar* groups, but similar in size to those of many other gibbon species. Presumably, the siamang's more folivorous diet permits smaller territories than expected for its larger body size (Gittins and Raemakers, 1980).

Compared with duets of other gibbon species, siamang duets exhibit a particular complex vocal structure (e.g. Lamprecht, 1970; Haimoff, 1981, 1983; Geissmann, 2000a, 2002a). Whereas most gibbon species appear to exhibit little paternal care (Fisher and Geissmann, 1990), it is quite pronounced in siamangs: several infant siamangs, both in the wild and captivity, have been observed being carried by their fathers (Alberts, 1983, 1987; Chivers, 1974; Dielentheis et al, 1991; Lee, 1976). Such carriage has been reported to begin in the second half of the infant's first year of life and to continue during the second year.

2. Material and Methods

2.1 Ethogram of White-Cheeked Crested Gibbons

For this research the following three reports have been studied prior to the observations on the white-cheeked crested gibbon group of Apeldoorn:

- *Das Verhaltensrepertoire des Weissswangen-Schopfgibbons (Hylobates leucogenys)* (Hold, 1998)
- *Paarbeziehung beim Siamang-Gibbon (Hylobates syndactylus)* im Zoo (Orgeldinger, 1999). In Table 1 this species is called *Symphalangus syndactylus*.
- *Patterns of gibbon behavior on Hall's island, Bermuda. A preliminary ethogram for Hylobates lar* (Baldwin and Teleki, 1976).

For the ethogram of white-cheeked crested gibbons, Hold (1998) has done research on four gibbon groups in three different zoos. The group size of all 4 zoos are shown in table 2. All four gibbon groups are situated on a gibbon island during the observation time.

Table 2. Group size and observation period of all groups studied by Hold (1998).

Zoo	Group size	Observation period	Combined observation time (hours)	
			per animal	per group
Amsterdam	1 couple	01.04 - 19.04 (1998)	42.0	84.0
Beekse Bergen	1 couple + infant	27.04 - 12.05 (1998)	26.0	78.0
Hannover 1	1 couple + infant	01.08 - 21.09 (1997)	25.5	76.5
Hannover 2	1 couple + infant + subadult	07.08 - 29.09 (1997)	22.5	90.0

Orgeldinger (1985) observed in total 57 siamangs for 2560 hours during the period from April 1985 till June 1993. The siamang data cover 12-14 groups (depending on variables) and the observation time per focal animal was 40 hours. Only 13 siamangs are situated on a gibbon island, the other 44 siamangs are observed in an inside or outside enclosure.

In this report, the ethogram of the white-cheeked crested gibbon previously made by Hold (1998) is completed with three other behaviour patterns after reading the ethogram of Baldwin & Teleki (1976, an ethogram of lar gibbons) and the ethogram of Orgeldinger (1999, an ethogram of siamang gibbons). These three behaviour patterns (**Stand**, **Sit** and **Lie**) are taken from the ethogram of lar gibbons (Baldwin and Teleki, 1976) and are grouped into the general category **Stationary position**. This category was not mentioned by Hold (1998), but is performed by every gibbon.

The complete ethogram consists out of 81 major behaviour elements and is grouped into 14 general categories (Appendix 1). Each distinct element is designated by a type number as well as a word or phrase label. This ethogram is useful for observing gibbons on an island.

1. Interaction between Adults and Infants

- 01. Take nipple in mouth (NM)
- 02. Belly carrying (BC)
- 03. Bring in the infant (BI)
- 04. Reprimand the infant (RI)

2. Locomotion

- 05. Swing/hang (Sw)
- 06. Make a tumble (MT)
- 07. Somersault (So)
- 08. Jump (Ju)
- 09. Climb (Cl)
- 10. Free fall (FF)¹
- 11. Brachiate (Br)
- 12. Tumble around the rope (TR)
- 13. Cower (Co)
- 14. Swing on one arm (SA)
- 15. Walk bipedal (WB)

3. Object Behaviour

- 16. Explorative grab at objects (EO)
- 17. Research object (RO)
- 18. Bite in object (BO)
- 19. Get the object out of the water (OW)
- 20. Throw up and catch the play object (TuO)
- 21. Throw away respectively up the play object (TaO)
- 22. Object play (rope/stick) (OR/S)
- 23. Play with grass (PG)
- 24. To lay about the object (LO)

4. Territorial Behaviour

- 25. Inhibited bite (IB)
- 26. Grab at social partner (GP)
- 27. Grab at bird (GB)
- 28. Romp bite (RB)
- 29. Quick chase play (QCP)
- 30. Quick chase aggressive (QCA)¹
- 31. Push oneself between two animals (PA)
- 32. Observe (Ob)
- 33. Reprimand the animal (RA)
- 34. Threat bite (TB)
- 35. Threaten (Th)

5. Impress Behaviour

- 36. Wild impress swing (WS)
- 37. Pirouette (Pi)

6. Food Supply

- 38. Grab grass (GG)
- 39. Catch food (CF)
- 40. Catch insects (CI)
- 41. Transport food (TF)
- 42. Taste food (TF)

- 43. Remove food (RF)
- 44. Grab food (GF)
- 45. Soak bread (SB)
- 46. Lick off vegetation (LV)
- 47. Bite off vegetation (BV)
- 48. Break off vegetation (BrV)
- 49. Lick off water-drops (LW)

7. Food Consume

- 50. Drink (Dr)
- 51. Eat (Ea)

8. Excretion

- 52. Urinate (Ur)
- 53. Defecate (De)

9. Rest Behaviour

- 54. Rest (Re)¹
- 55. Doze (Do)
- 56. Sleep (Sl)

10. Intragroup Behaviour

- 57. Body contact (BC)
- 58. Embrace (Em)
- 59. Invite for social grooming (ISG)
- 60. Allogrooming (AG)

11. Comfort Behaviour

- 61. Lick off finger (LF)
- 62. Lick off arm (LA)
- 63. Bodyshake (Bs)
- 64. Scratch (Sc)
- 65. Stretch (St)
- 66. Shake out the hand (SH)
- 67. Autogrooming (AuG)
- 68. Pull out hair/skin (PH)
- 69. Clean fingernail (CF)
- 70. Rub the nose (RN)
- 71. Yawn (Ya)
- 72. Sneeze (Sn)

12. Sexual Behaviour

- 73. Penis manipulation (PM)¹
- 74. Invite for anogenital inspection (IAI)
- 75. Anogenital inspection (AI)
- 76. Copulation (Co)
- 77. Refuse copulation (Rc)

13. Acoustic Communication

- 78. Acoustic communication

14. Stationary Position

- 79. Stand
- 80. Sit
- 81. Lie

2.2 Animals

The animals which have been observed for this research live at the Apenheul Zoo since summer 2001. The group composition is shown in Table 3. The age classes used here, are those proposed by Geissmann (1991) for gibbons kept in captivity: infants 0-2 years; juveniles 2.1-4 years; subadults 4.1-6 years, adults older than 6 years.

Table 3. Group composition of the gibbon group of Apenheul.¹

Name	Sex	Age	Age class	Date of birth	Place of birth	Former zoo
Kanak	F ¹	10	Ad. ¹	18 Sept. 1993	La Fontaine	La Fontaine
Yunnan	M ¹	7	Ad.	30 Oct. 1996	Hannover	Hannover & Plankendael
Kirin	M ¹	1.5	Inf.	10 Feb. 2003	Apeldoorn	

¹ Abbreviations: F = Female, M = Male; Ad. = Adult, Inf. = Infant.

2.3 Enclosure

During daytime, the gibbon group of Apeldoorn spend their time on an island which is completely overgrown by natural vegetation. This island covers an area of about 250 m². At night and during the winter season (from November until about mid-March), the gibbons are kept in an indoor enclosure which is connected to the island by a small bridge. The indoor enclosure has an area of 15 m². At about 09:00 in the morning, the gibbons are being released on the island, where they are left until 17:00. During the day, they are fed three times, but during high season, they sometimes receive extra food twice. In the morning at 08:30, each gibbon gets one “gibbon ball and two pieces of chicory before they are being released on the island. At 13:00, they obtain 2 apples and 1 carrot on the island, and at 16:00 they obtain 4 apples, chicory or endive, a half of paprika or a piece of a cucumber and two pieces of sweet fruit in the indoor enclosure.

Monday:	1 hand of scraps, 2 tomatoes, pieces of celery
Tuesday:	2 pieces of bread, 1 onion
Wednesday:	Nuts, piece of celery
Thursday:	2 pieces of bread, a piece of cabbage
Friday:	2 boiled eggs, ½ leek
Saturday:	2 boiled potatoes
Sunday:	A piece of diet cheese, piece of cabbage

The island is long drawn, and visitors are able to view the gibbons from a few different places but are not able to walk around the whole island. If a gibbon is situated at the back of the island, the gibbon is hardly visible for visitors. The cleaning of the enclosure takes place daily at around 9.30h. and it takes about 10 minutes.



Figure 2. Gibbon island of Apenheul Zoo

2.4 Observation Methods

The observation methods used during this research are being described by Martin & Bateson (1993). The following two techniques are applied:

Scan Sampling

The scan sampling is applied to record the spatial division of an individual in a group (individual distances) divided over a day. The individual distances between each group member are divided into 4 distance classes: 0 m (body contact); 0.1 – 1 m; 1.1 – 3 m; and >3 m. Every group member is being scanned at the same time every 5 minutes by instantaneous sampling for 28 hours each animal. In total the number of scans are 1008.

Focal Animal Sampling

Focal animal sampling means observing one individual (or one dyad, one litter or some other unit) for a specified amount of time and recording all instances of its behaviour – usually for several different categories of behaviour (Martin & Bateson, 1993). The focal animal is being changed every 30 minutes. The frequency and the exact behaviour pattern are taken down. The time which is spent on focal animal sampling is shown in table 4.

Table 4. Duration of the observations with focal animal sampling

Group	Observation time and period	Duration of a focal animal observation (minutes)	Combined observation time (hours)	
			per animal	per group
Apeldoorn	09:00 – 16:30, 26 July – 09 Aug. 2004	30	28	84

2.5 Statistic Analyses

For the statistical analysis of the differences between the behaviour of the male and the female, and the differences between the age-classes, the Chi-Square test is being used. For the comparison between the two age-classes both the male adult and the female adult have been compared separately with the infant. The Chi-Square test detects whether there is a significant association between two categorical variables. However, it does not say anything about how strong that association might be (Field, 2000). Table 5 shows the significance criteria used.

Table 5. Significance vale used

Significance level	Error probability
Not significant	$p > 0.05$
Slightly significant	$p < 0.05$
Significant	$p < 0.01$
Highly significant	$p < 0.001$

Also for the research question “Do the individual distance classes of the white-cheeked crested gibbon group at Apenheul correspond with the individual distance classes of the 4 white-cheeked crested gibbon groups studied by Hold (1998)?”. the Chi Square test is being used for the statistic analyses. In this case ‘Not significant’ is: $p > 0.016$. ($0.05/3 = 0.016$).

2.6 Technical Appliances

For the short video clips of the behaviour patterns a Sony TRV145E digital video camcorder was used.

3. Results

3.1 The Revised Ethogram

Appendix 1 provides the following information for each display behaviour of the revised ethogram:

Definition, i.e. a description of the behaviour pattern.

Context, i.e. situations in which the behaviour occurred with relatively high probability.

Comments, i.e. discussion of the use of behaviour in the Apenheul gibbon group. These notes on the behaviour's causation and possible functions complement the qualitative analysis presented under 'Context'. This part may contain anecdotes and special analysis.

3.2 Evaluation of the Ethogram by Hold (1998)

Is the ethogram of white-cheeked crested gibbons (Hold, 1998) complete and representative, or are there any behavioural elements that should be mentioned, but are missing in this ethogram? If so, which ones?

The ethogram of white-cheeked crested gibbons (Hold, 1998) closely corresponds to the one found in this study and is nearly complete. A total seven behaviour elements have been added to the ethogram of Hold. Three behaviour elements **Stand (St)**, **Sit (Si)** and **Lie (Li)** are added before doing observations for this research. These behaviour elements are categorised as **Stationary posture**. Four of these seven behaviour elements (**Quick chase aggressive (QCa)**, **Free fall (FF)**, **Rest (Re)**, and **Penis manipulation (PM)**) are added to the ethogram of Hold after doing some pre observations on the gibbon group at Apeldoorn. These four behaviour patterns were seen during the time of the pre observations.

The behaviour elements **Quick chase aggressive (QCa)**, **Stand (St)**, **Sit (Si)** and **Lie (Li)** are taken from the ethogram of Lar gibbons (Baldwin and Teleki, 1976) and the other 3 behaviour patterns (**Free fall (FF)**, **Rest (Re)**, and **Penis manipulation (PM)**) are taken from the ethogram of siamang (Orgeldinger, 1999).

3.3 Behaviours only observed in Apenheul

Does the gibbon group in Apenheul show any typical behaviour that only occurs in this specific gibbon group and has not been observed in the four gibbon groups observed by Hold (1998) and is not mentioned in the ethograms for siamangs (Orgeldinger, 1999) and white-handed gibbons (Baldwin and Teleki, 1976), respectively? If so, which behaviours are those?

During the observation period of two weeks, the white-cheeked crested gibbon group at Apeldoorn only showed two typical behavioural elements that have not been observed in the four gibbon groups studied by Hold (1998). These two behavioural elements are:

Jerky Body Movement (JBM)

The female performed jerky body movements with her upper or whole body. During the whole observation period it has been observed that the female performed this behaviour 70 times. She showed this behaviour mostly if the male and infant were playing together while the female was nearby. In the following situations the female also showed these jerky body movements occasionally:

- Just before feeding time.
- When the male is sitting close (< 2m) behind her.

- After copulation.

This behaviour pattern has only been observed by the female and has never been observed by both the male and infant.

[This behaviour was observed in siamangs by Orgeldinger (1999, p. 60: “Ruckartiges Körperbewegen”).]

Sliding down a Rope/Tree-Trunk (SD)

The animal is holding itself with its hands and feet onto a rope or tree-trunk and slides downwards to a lower level.

Both the male and infant showed this behaviour element (Sliding down a rope/tree-trunk) a few times. The male performed this behaviour four times and the infant two times. It has not been observed by the female.

3.4 Behaviours not observed in Apenheul

Are there any behavioural elements exclusively shown by the four groups of white-cheeked crested gibbons observed by Hold (1998) and has not been seen in Apenheul? If so, which behavioural elements are these?

Seven behavioural elements are exclusively shown by the four groups of white-cheeked crested gibbons observed by Hold (1998). The frequencies of these elements are shown in Table 6.

Table 6. The frequencies of the behaviour elements which have been performed exclusively by the gibbon groups observed by Hold (1998).

Behaviour element	Hold (1998)											
	Amsterdam		Beekse Bergen			Hannover 1			Hannover 2			
	M	F	M	F	I	M	F	I	M	F	I	S
To lay about the object	0	0	3	0	1	0	0	0	0	0	0	0
taste food	0	0	2	2	0	0	0	0	0	0	0	0
Soak bread	0	0	1	3	0	0	0	0	0	0	0	0
Lick off vegetation	0	0	0	0	0	0	0	4	0	1	5	1
Lick off water-drops	0	0	0	0	4	24	12	22	0	5	3	3
Sleep	0	0	1	0	0	0	0	0	0	0	0	0
Pull out hair/skin	0	0	0	0	0	0	1	1	1	2	0	1

¹ **Abbreviations:** M = male, F = Female, I = Infant and S = Subadult.

These behaviour elements were only performed occasionally by a few animals and have not been performed in every group. Gibbons sleep at night, so this behaviour is not performed during daytime when the observations have been done.

3.5 Comparison of Individual Distance Classes

Do the individual distance classes of the white-cheeked crested gibbon group at Apeldoorn correspond with the individual distance classes of the 4 white-cheeked crested gibbon groups studied by Hold (1998)? A comparison has been made between groups which have the same group composition. Two gibbon groups studied by Hold (Beekse Bergen and

Hannover 1) have the same group size as the gibbon group of Apeldoorn. These three groups consist of a couple with an infant. The relative frequencies in % of the individual distance classes of these three white-cheeked crested gibbon groups are shown in Figure 2. For the statistical comparison the Chi-Square test is being used.

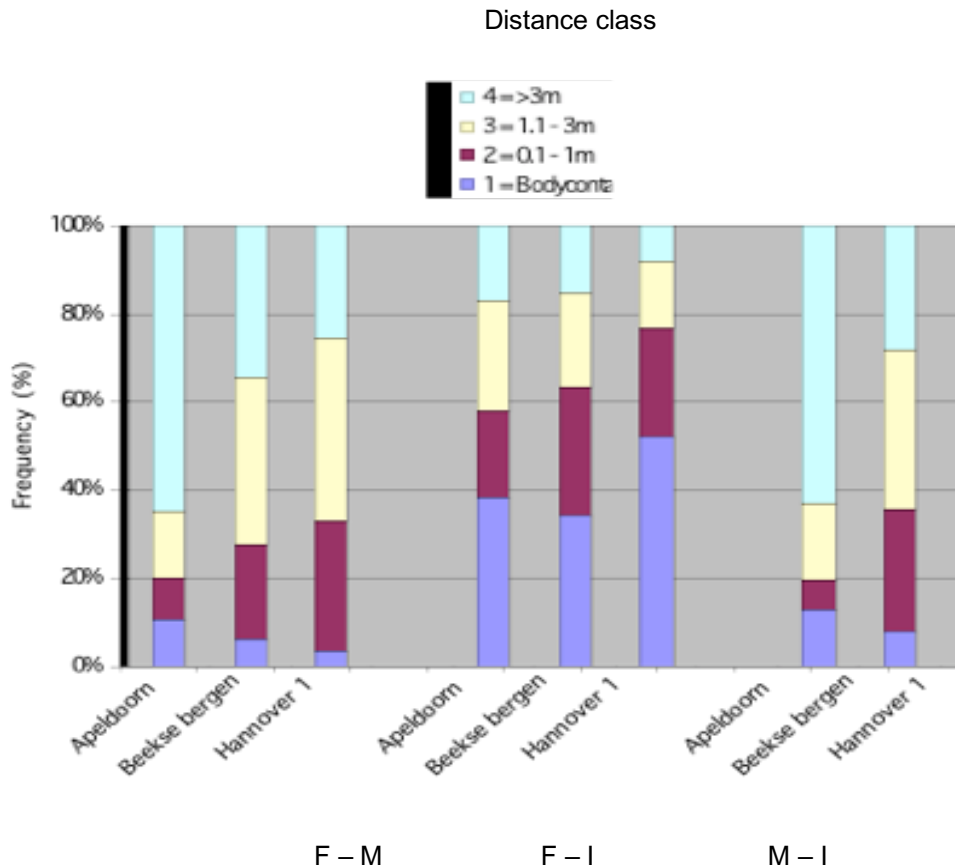


Figure 3. Various classes in percent with every possible dyad, clustered by age classes. Abbreviations: F = Female, M = Male, I = Infant.

Figure 3 shows that the mother and infant spend most of the time close to each other. In all 3 groups the females and infants have the most body contact. Less than 20% of the time they spend more than 3 meters away from each other.

In Table 7 a statistic comparison is made between the three gibbon groups for every dyad.

Table 7. A statistic comparison (Chi-Square test) of distance classes between the three gibbon groups.

Dyad	Difference	
	Significant $p < 0.016$	Not significant
Apeldoorn - Beekse Bergen		
Female - Male	X	
Female - Infant		X
Male - Infant	X	
Apeldoorn - Hannover 1		
Female - Male	X	
Female - Infant	X	
Male - Infant	X	
Beekse Bergen - Hannover 1		
Female - Male		X
Female - Infant	X	
Male - Infant		X

The group of Apeldoorn and Hannover 1 do not correspond with each other. In all three possible dyads (Female – Male; Female – Infant and Male – Infant) they differ highly significant from each other. The gibbon groups observed by Hold (Beekse Bergen and Hannover 1) only differ from each other in one dyad (Female – Infant).

The absolute and relative frequencies of the in this case study defined distance classes for all possible dyads are listed in Appendix 2. All four gibbon groups studied by Hold (1998) and the group of Apeldoorn observed during this study are listed there.

3.6 Comparison between Male and Female

For this part of the research only the male and female of the gibbon group of Apeldoorn have been compared. There are a few differences between the behaviour of the male and female. The frequencies of all behavioural elements are shown in Appendix 3 (absolute frequency). The statistical comparison (Chi-square test) between male and female are listed in Appendix 4.

Appendix 4 shows that 18 behavioural elements show a high significant ($p < 0.001$) difference in frequency between male and female. Table 8 lists the 12 behavioural elements that have been performed significantly more in absolute frequency by the male compared to the female.

Table 7. The absolute frequencies of behaviour elements which have been performed significantly more by the male (Chi-Square test).

Category	Behaviour element	Absolute frequency		Difference
		Male n = 1	Female n = 1	
Locomotion	Jump	98	27	71
	Brachiate	645	399	246
	Free fall	20	3	17
	Walk bipedal	86	57	29
Object behaviour	Bite in object	14	0	14
Territorial behaviour	Romp bite ¹	256	23	233
	Quick chase play ²	35	5	30
Food supply	Break off vegetation	206	115	91
Food consume	Eat	269	187	82
Comfort behaviour	Scratch	430	195	235
Stationary position	Sit	538	371	167
	Lie	42	15	27

¹ Romp bite: *The male and the infant play most of the time together. Occasionally the female joins them or plays with the infant alone.*

² Quick chase play: *While the male is playing together with the infant, the male chases the infant in a playful way.*

Table 8 shows that the following behaviour elements are performed at least 100 times more by the male than the female: **Brachiate**, **Romp bite**, **Scratch** and **Sit**, and that only one behaviour element (**Bite in object**) has been performed by the male only.

The seven behaviour elements that have been performed significantly more by the **female** are shown in Table 9.

Table 9. The absolute frequencies of behaviour elements that have been performed significantly more by the female (Chi-square test).

Category	Behaviour element	Absolute frequency		Difference
		Male n = 1	Female n = 1	
Interaction adult - infant	Belly carrying	0	11	11
Impress behaviour	Wild impress ¹	1	7	6
Rest behaviour	Doze	0	16	16
Intergroup behaviour	Body contact	46	475	429
	Allogrooming	62	110	48
Comfort behaviour	Lick off finger ²	20	51	31
-	Jerky body movements	0	70	70

¹ Wild impress: *The female is showing this behaviour element right after doing a great call.*

² Lick off finger: *The female licks off her finger every time after she has urinated. She moves her hand from her anus to her mouth and then licks off her finger. The male never licked off his finger after he urinates.*

It is obvious from the table that the female has a lot more **body contact** with the infant and that three behaviour elements (**Belly carrying**, **Doze** and **Jerky body movements**) were exclusively performed by the female.

3.7 Comparison between two Age Classes (Adult vs. Infant)

The gibbon group studied for this research consists of three members, which are grouped into two different age-classes; 2 adults (a couple) and an infant. The frequencies of all behavioural elements of the 2 adults and the infant are shown in Appendix 3 (absolute frequency). In Appendix 5 a statistic comparison has been made between these two age-classes.

Age-Class Infant

Five behavioural elements were observed by the infant only and were not performed by the adults (Table 10).

Table 10. Behaviour elements that were only performed by the infant (Chi-square test).

Category	Behaviour element	Absolute frequency Infant n = 1
Interaction between adult and infant	Take nipple in mouth	489
Object behaviour	Throw up and catch the object	17
Territorial behaviour	Push oneself between two animals	6
Impress behaviour	Pirouette	4
Food supply	Remove food	19

The following 8 behaviour elements are performed significantly more by the infant compared to both adults (Table 11).

Table 11. The absolute frequencies of behaviour elements which have been performed significantly more by the infant Chi-square test).

Category	Behaviour element	Absolute frequency		
		Infant N = 1	Adult Male n= 1	Female n = 1
Locomotion	Jump	444	98	27
	Climb	668	250	190
	Brachiate	907	645	399
	Free fall	97	20	3
	Cower	277	145	113
	Swing on one arm	278	86	57
	Walk bipedal	353	201	60
Object behaviour	Object play rope/stick	75	5	0

From this table it is obvious that the infant performs significantly more those behaviour elements which are grouped into the category '**Locomotion**'. The infant is more active then both adults.

Age-Class Adult

13 behaviour elements were observed only by adults and were not performed by the infant (Table 12).

Table 12. Behaviour elements only performed by the adults and not by the infant (Chi-square test).

Category	Behaviour element	Absolute frequency	
		Male n = 1	Female n = 1
Territorial behaviour	Threat bite	2	0
	Threaten	1	0
Food supply	Catch food ¹	7	12
Rest behaviour	Doze	0	16
Comfort behaviour	Body shake	9	1
	Stretch	7	0
	Shake out hand	3	0
	Autogrooming	5	11
Sexual behaviour ²	Clean fingernail	2	0
	Penis manipulation	1	0
	Invite for anogenital inspection	0	10
	Anogenital inspection	3	4
	Copulation	15	27
	Refuse copulation	0	1
	Jerky body movements	0	70

¹ Catch food: Only both adults can catch food which is thrown onto the gibbon island by the animal keeper. The female shares her food with the infant.

² Sexual behaviour: The infant does not perform any sexual behaviour.

The behaviour elements that are performed significantly more by both adults than by the infant are shown in Table 13.

Table 13. The absolute frequencies of behaviour elements which have been performed significantly more by both adults than by the infant (Chi-square test).

Category	Behaviour element	Absolute frequency		
		Infant n = 1	Adult	
			Male n = 1	Female n = 1
Territorial behaviour	Observe	81	199	144
Rest behaviour	Rest	1	27	34
Communication	Vocalisation	2	18	23
Stationary posture	Sit	210	538	371

3.8 Differences between White-Cheeked Crested Gibbons and Siamangs

This section compares the siamang ethogram (Orgeldinger, 1999) to the ethograms of white-cheeked crested gibbons (Hold, 1998 and this study). There are two main differences between these two ethograms, namely:

The ethogram of the siamang gibbons is far more comprehensive than the ethogram of the white-cheeked crested gibbons. The siamang ethogram consists of 188 behaviour patterns, which are grouped into 11 general categories. And the white-cheeked crested gibbon ethogram consists of 83 behaviour patterns, which are grouped into 14 categories (Table 14).

Table 14. The general categories of both ethograms.

General categories			
White-cheeked crested gibbon	Number of behavioural elements	Siamang	Number of behavioural elements
<i>Interaction between adult and infant</i>	4	<i>Caretaking for young</i>	16
Locomotion	10	Locomotion	9
<i>Object behaviour</i>	9	<i>Play behaviour</i>	39
Territorial behaviour	11	Territorial behaviour	22
<i>Impress behaviour</i>	2		
Food supply	12	Food supply	10
<i>Food consume</i>	2		
Excretion	2	Excretion	2
Rest behaviour	3	Rest behaviour	4
Intergroup behaviour	4	Intergroup behaviour	50
Comfort behaviour	12	Comfort behaviour	15
Sexual behaviour	5	Sexual behaviour	14
<i>Acoustic behaviour</i>	1		
Stationary position	3	Position posture	5

Two categories (*Interaction between adult and infant* and *Object behaviour*) have a different description but do correspond with each other. These two categories are written *Italics*. And three categories (***Impress behaviour***, ***Food consume*** and ***Acoustic behaviour***) are only mentioned in the white-cheeked crested gibbon ethogram.

In the white-cheeked crested gibbon ethogram are, in comparison with the siamang ethogram, in the following five general categories less behavioural elements subdivided into one category.

- Interaction between adult and infant/Caretaking for young (4 – 16)
- Object behaviour/Play behaviour (9 – 39)
- Territorial behaviour (11 – 22)
- Intergroup behaviour (4 – 50)
- Sexual behaviour (5 – 14)

All behavioural elements of the siamang ethogram are listed in Appendix 7.

The second main difference between these two ethograms is: In the siamang ethogram some elements are mentioned in more than one category. In the white-cheeked crested gibbon ethogram every behaviour element is mentioned in only one category.

3.9 Behavioural Elements Exclusive to White-Cheeked Crested Gibbons or Siamangs

All behavioural elements of the siamang ethogram are listed in Appendix 7. This table indicates if a behaviour element of the siamang ethogram is represented in the white-cheeked

crested gibbon ethogram of this study. In total 106 behavioural elements are not represented in the white-cheeked crested gibbon ethogram. However this does not mean that these 106 behavioural elements are exclusive to the siamang gibbon. The siamang ethogram is far more comprehensive, the most general categories are subdivided into more brief behavioural elements. For example the category **sexual behaviour** is divided into 14 behavioural elements. Behaviour elements like Penis erection, Copulation face, oral stimulation of the penis by female, oral stimulation of the female genital area by male, copulation face, copulation sound and slow chase are being separately described in the siamang ethogram, but are not mentioned separately in the white-cheeked crested ethogram.

Appendix 8 shows a list with all behavioural elements mentioned in the white-cheeked crested ethogram of this study. A comparison has been made between the siamang and white-cheeked crested gibbon ethogram. The following behavioural elements are exclusive to the white-cheeked crested gibbons (Table 15).

Table 15. Behaviour elements exclusively performed by the white-cheeked crested gibbons.

Category	Behaviour element
Object behaviour	Get the object out of the water ¹
	Sliding down rope/tree-trunk
	Play with grass ¹
	Object play rope/stick
	To lay about the object
Territorial behaviour	Grab at bird ¹
Food supply	Grab grass ¹
	Lick off vegetation ¹
	Bite off vegetation ¹
	Break off vegetation ¹
	Catch food ²
Comfort behaviour	Sneeze
	Jerky body movements ³

¹ These seven behavioural elements can only be performed if the animal is housed on an island. All five white-cheeked crested gibbon groups are observed on a gibbon island, whereas most siamang gibbons are observed in an inside or outside enclosure. If all siamang gibbons were also being observed on a gibbon island they would probably also perform these behaviours.

² Catch food: Food is being thrown on the island by the animal keeper. This is the reason why the white-cheeked crested gibbon is performing this behaviour. In an inside and outside enclosure food is not being thrown by the animal keeper.

³ Jerky body movements: Only one white-cheeked crested female gibbon (Apeldoorn) performed this behaviour. This behaviour is not mentioned in the white-cheeked crested gibbon ethogram of Hold.

There are no major differences between the siamang and white-cheeked crested gibbon.

4. Discussion

4.1 Comparison between White-Cheeked Crested Gibbon Groups

In this section, I compare the white-cheeked crested gibbon group of Apeldoorn (this study) with the four white-cheeked crested gibbon groups observed by Hold (1998). An ethogram is never complete. The present ethogram's limitations are obvious. It is based on the behaviour of 15 white-cheeked crested gibbons in captivity and studied for a relatively short period of time. This ethogram should be seen as a starting point, intended to stimulate and assist further studies of white-cheeked crested gibbon behaviour.

Behaviour

The results of the comparison between the various gibbon groups can be influenced by several factors like:

- a) The surrounding in which the animals are being kept. (different zoos)
- b) The weather circumstances during the observations.
- c) Individual animal.

The gibbons stay in various zoos, because of this the circumstances of every group differs from each other. The size of the gibbon island, the vegetation off the island and even the number of visitors can influence the behaviour of an animal. It can happen that a certain behaviour only occurs in one particular group, because other groups do not have the possibility to perform that certain behaviour. The following three behaviours are an example of this case: Soak bread, lick off vegetation, and lick off water-drops.

- If an animal does not receive bread as food, it can not perform the behaviour "soak bread".
- If it does not rain during the whole observation period, the animal does not have the opportunity to lick off water-drops and it probably will not lick off vegetation.

The weather can also influence the behaviour of a gibbon. During rainy days they will be less active than during dry days. The performance of behaviour can also be dependent on an individual; every individual has its own character. Besides the behaviour will also depend on if both animals get along with each other or not.

Individual Distance Classes

With the comparison of the individual distance classes between the gibbon groups observed by Hold and the gibbon group observed during this research only a comparison has been made between these groups with the same group size. This means only three (Apeldoorn, Beekse Bergen and Hannover1) of the five groups in total have been compared with each other. The spatial division of an individual in a group can be influenced by:

- The size of the enclosure.

The larger the enclosure (island), the further the individual can stay away from each other. In a small enclosure the animals do not have the opportunity to stay more than a certain distance away from each other.

- How long the animals have been together/ The strength of the pair bond.

A male and female gibbon which have only been placed together for a short time probably have a less strong pair bond than a couple which have been together for a longer period of time. A couple with a less strong pair bond will most likely spend less time together than a couple with a stronger pair bond.

The spatial division between a mother and its infant depends most likely on the age of the infant. The younger the infant the more dependent the infant is of its mother and so the closer the relation between the mother and infant is.

From the results it appears that the Female – Infant bond is the strongest off all three dyads (Female – Male, Female – Infant, and Male – Infant). From Appendix 2 it can also be concluded that the Female – Infant bond is the strongest bond within the group even if the group consists of 4 members (couple + infant + subadult). The male of this particular group has very few till no body contact at all with other members of the group. However this does not say anything about the individual distances of the male in general in bigger groups. It says more about this certain male itself.

The significant differences of every dyad between the gibbon group of Apeldoorn and the group of Hannover 1 can also be affected by the three factors mentioned above; the surrounding, weather and individual animal.

4.2 Comparison between Sex and Age Classes

The results in this comparison only say something about the behaviour of the three gibbons kept at Apeldoorn. No conclusion can be made for the male, female and infant of this species in general, because the number of individuals is too small.

Comparison Male – Female

It becomes evident from the results that the male is more active compared to the female. The male jumps, brachiates and walks bipedal significantly more. Despite of the less time the male spends with the infant, the male plays significantly more with the infant than the female does. On the contrary the results also show that the male is sitting more often than the female. These data are deceptive however. If the duration of this behaviour had been registered, it would become obvious that the female is sitting for a longer period of time in the most cases. The male is three years younger than the female and only 7 years of age, barely an adult. According to Geissmann (1991) the age classes for gibbons kept in captivity are: Infants 0-2 year; juvenile 2,1-4 year; subadult 4,1-6 year and adult older than 6 year. This can probably explain why the male is more active and more playful than the female.

Another obvious difference between the male and female is, is that the female is grooming another individual more then the male. In 75% of all cases the female grooms another gibbon whereas the male only in 20% of the cases grooms the female or infant. The data of Hold (1998) also reveals that the female of each group grooms another animal more than the male. Perhaps grooming can be explained as a form of nursing behaviour. In a white-cheeked crested gibbon family the female is the one which is nursing the infant, especially during the first year of the infant's life, the male rarely takes part in it. This can be a reason why a female grooms another animal more often than a male.

Comparison Adult – Infant

In this case two adults (male and female) have been compared with the infant. Like with the comparison between the sex, the number of animals (n=3) observed during this research, is far too less to make any general conclusion for this species. The results only refer to these three observed gibbons. The infant is obviously more active (he jumps, climbs, brachiates, walks and plays alone or together with the male or female) than both adults. This can be explained by the age. The infant of this gibbon group (Apenheul) is during the time of the observations 15 months old of age and is already becoming less dependent of the mother and starts to explore the surrounding by itself. The father becomes closer with the infant by playing together.

4.3 Comparison between Siamang and White-Cheeked Crested Gibbons

This section compares the siamang ethogram (Orgeldinger, 1999) to the ethograms of white-cheeked crested gibbons (Hold, 1998 and this study).

A few factors make a comparison between these two ethograms difficult. These factors are:

The siamang ethogram is far more comprehensive than the white-cheeked crested gibbon ethogram, the most general categories are subdivided into more brief behavioural elements. Also some behavioural elements are mentioned in various general categories, whereas in the white-cheeked ethogram every behaviour element is only mentioned in one category.

Most siamangs are observed in an inside or outside enclosure. Only 3 out of in total 12 observed siamang gibbon groups are situated on a gibbon island (see Appendix 8). In contrast, all five white-cheeked crested gibbon groups were kept on islands. The different living conditions influence the behaviour. Most indoor/outdoor enclosures are much smaller than a gibbon island. A small enclosure may contribute to the performance of more stress related behaviour. Secondly the gibbon islands are designed more naturally than an indoor/outdoor enclosure. Animals which are kept on an island have the opportunity to perform more natural behaviour elements (like climbing, brachiating and foraging in a tree) than gibbons which are being held in an enclosure. Gibbons kept on an island are being observed from a larger distance. The distance between the observer and animal are in most cases shorter if the animals stay in an inside or outside enclosure and so the animals are better visible. In that case the facial expressions are also better visible.

There are differences in number of observed individuals. For the siamang ethogram, 57 siamangs of all age classes have been observed, whereas for the white-cheeked crested gibbon ethogram a total 15 gibbons have been observed. For the white-cheeked crested gibbon ethogram, no juveniles and only one subadult were included. It is possible that if some juveniles and subadults were included during the observations they would perform behaviour elements which have not been observed in the other age-classes.

5. Conclusions

The ethogram of white-cheeked crested gibbons (Hold, 1998) closely corresponds to the one of this study and is nearly complete. In total nine behaviour elements have been added to the ethogram of Hold. Two behaviours have exclusively been observed in the group of Apeldoorn. The female of this gibbon group performed 'Jerky body movements' (70 times in total) and both the male and infant of this group performed 'Sliding down a rope/tree-trunk'. The female performs jerky body movements with her upper or whole body mostly if the male and infant are playing together while the female is nearby. Occasionally she also exhibits this behaviour just before the animal keeper is throwing food on the island, or when the male is sitting close ($< 2\text{m}$) behind her, or after copulation.

This study shows that the mother-infant is by far the strongest bond within a white-cheeked crested gibbon group. Less than 20% of the time the infant stays more than 3 meters away from the mother. The behaviour of the male and female do not differ a lot from each other. The most obvious difference is that only the female is nursing the infant, carrying the infant on her belly, and sharing her food with the infant. The male spends time with the infant by playing with it; the male does not carry the infant on his belly nor does he share his food with the infant. The female is only playing occasionally with the infant. Both the male and infant are far more active than the female.

The present study shows that the behavioural elements of the siamang and the white-cheeked crested gibbons are fundamentally similar. A statistical comparison between these two ethograms is difficult for three reasons. (1) the siamang ethogram is far more comprehensive than the white-cheeked crested gibbon ethogram, (2) the living conditions of these two gibbon species differ from each other and (3) the numbers of observed individuals differs from each other.

It is recommended that future observations should include white-cheeked crested gibbon families with a juvenile and subadult group members, as well.

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Appendices

Appendix 1: Ethogram of the White-Cheeked Crested Gibbon

This is the ethogram for white-cheeked crested gibbons made by Hold (1998), supplemented by seven behavioural elements from the present study.

1. Interactions between adult and infants

01. Take nipple in the mouth (NM)

The infant takes the nipple in the mouth. Suck movements are on account of big distance between observer and focal animal not always to observe. This behaviour element can be stretched out for a longer period of time and can contain nipple change.

Function: Feeding/ maternal vicinity

02. Belly carrying (BC)

The infant is hanging ventro-ventral on the belly of the mother; the legs lay in the groin area, the arms comprise the body of the mother almost completely, the head lies within the reach of the chestbone. The hands clasped to the back skin of the female. Meanwhile the mother can carry out every locomotion form.

Function: Carry the infant. Cover distances, which the infant can not manage by itself.

Comment: Only the female was carrying the infant on her belly and never the male. The female was only carrying the infant when something unusual happened, like once when the gorillas were making loud noise or a plain was flying over very low. Also when the gibbons were getting fed on the island and the female and infant were far away from the feeding place, the female was carrying the infant at times.

03. Bring in the infant (BI)

The mother brings the infant to her. The mother lays her hand in the neck of the infant or grabs an arm and pulls the infant to her. This behavior element is mostly succeeded by BC.

Function: Protect the infant. Invite gesture to the infant.

04. Reprimand the infant (RI)

This behavior will be carried out in different ways for all animals of a group. It can be expressed in a slightly kick of the infant, a touch in the neck of the infant with a slightly opened mouth or push the infant away with the hand.

Function: A request of the mother animal to keep the infant calm during social grooming. Reprimand the infant on account of repeated '*Grab at a social partner*' (25). The mother points out the infant from her in account of '*Taking the nipple in the mouth*' (01) and '*belly carrying*' (02) for too long.

2. Locomotion

05. Swing/hang (Sw)

An animal is holding itself with both hands on a branch or rope and swings back and forward, or the animal is hanging calmly. An animal is sitting on a rope and swings back and forward.

Function: Behaviour element during playing. Play movement for other locomotion elements. Observe the surrounding from a flexible position.

06. Make a tumble (MT)

An animal makes a tumble on the ground (backwards or forwards).

Function: Play movement on the ground of the island. Concerning adult animals any possible missed behaviour.

07. Somersault (So)

An animal makes a somersault forwards. The somersault is carried out directly on the ground of the island.

Function: Play movement on the ground of the island.

08. Jump (Ju)

An animal is pushing himself up with both legs from a substratum and jumps to another island point. This behavior element is mostly going together with to conquer a height distance or a horizontal distance.

Function: Cover distances. Element in play movement.

Comment: During playing in the hammock, the infant jumped frequently from the rack into the hammock.

09. Climb (Cl)

An animal uses hands and feet, to reach a higher or lower elevation.

Function: Cover height distances.

10. Free fall (FF)

The animal lets itself fall (till 8m) and ends the fall by grabbing a branch.

Function: Cover distances.

11. Brachiation (Br)

An animal uses both arms in turns, to move himself by swinging along and under the chosen horizontal object. Brachiating can occur on a branch or rope. This behaviour element can also take up a stereotypic form, when over a long period of time the same movement is being repeated.

Function: Conquer distances. It can appear as a component of *Wild impress-brachiation* (34), *Quick chase* (28) or play behavior elements.

12. Tumble around the rope/branch (TR)

The animal tumbles forwards around a horizontal rope or branch, while it holds himself with both hands.

Function: Play movement

13. Cower (Co)

The animal is hanging with both hands on a branch or a horizontal stretched rope, swings backwards and up, raises the legs between the arms and sits eventually on the rope or branch

Function: Movement element, which results in a higher position.

14. Swing on one arm (SA)

An animal swings with one hand on a branch and swings active or passive to and fro. This behaviour pattern can be followed by vocalization, an impress action or play.

Function: Impress behavior pattern.

15. Walk bipedal (WB)

The animal goes or walks upright on the ground, on a rope or a branch and puts his feet down by turns. Besides the arms can hang down, sideways the body or hold up above the head.

Function: Conquer distance. Impress behaviour element.

Comment: If the male is walking on the ground, on a branch or on a rack, he mostly also uses one of his arms to touch the substrate. This is called tripedal walk.

3. Object behaviour

16. Explorative grab at objects (EO)

The animal grabs in a playful way at objects in his reach.

Function: Be aware of the environment, boredom, curiosity.

17. Research object (RO)

The animal grabs with one or both hands/feet at an object.

Function: Be aware of the environment, looking for food.

18. Bite in object (BO)

An animal bites in a thing, chews on it or uses it as a play object. This behavior pattern can be integrated in an object play.

Function: Play behavior, test the edibility.

19. Get the object out of the water (OW)

The animal is holding itself with one or two limbs on bushes and bows the upper body above the water, to reach the object in the water with one hand. The object can also be near the island, that the animal can reach the object from a seated position.

Function: Explore the environment, obtain food.

Comment: Once the male went into the water with his whole leg to get an object out of the water.

20. Throw up and catch the play object (TuO)

An animal throws up a play object over a short (5cm) or a bit higher (1m) distance or just lets it drop, to catch it before it reaches the ground. This behavior pattern is mostly repeated.

Function: Object play.

Comment: The infant occasionally threw up and caught a small stick.

21. Throw away (respectively up) the play object (TaO)

The animal throws an object, play object, or food away, respectively up.

Function: Object play.

22. Object play (rope/stick) (OR/S)

The animal grabs at the end of a rope and pushes it in regular distances, so that it swings to and fro. A stick is being touched and held tight with one or two limbs. The other limbs grab a stick, and once in a while the animal bites in the object. The animal can show combined locomotion types with this behavior pattern.

Function: Play behavior.

23. Play with grass (PG)

The animal pulls out blade of grass out of the ground and throws it in the air, continued by trying to catch the blade.

Function: Play behavior

24. To lay about the object (LO)

The animal is standing upright with an object (stick) in the hand. The stick is being beaten on the ground with the arms stretched widely.

Function: Play behaviour, impress behaviour.

4. Territorial- and play behaviour

25. Inhibited bite (IB)

An animal bites lightly (inhibited) another animal of the group in the hand or another part of the body. The bitten animal does not show any sign of pain.

Function: Play behavior, reprimand, and excitement of attention.

26. Grab at social partner (GP)

An animal grabs at a social partner. This action can be calm, but can also be aggressive.

Function: Get attention from another animal.

Comment: The female grabbed the infant once when the infant wanted to leave after he was groomed by the female.

27. Grab at bird (GB)

An animal grabs at a bird, which is situated on the island.

Function: Play behavior, territorial behavior.

Comment: The male four times tried to grab a bird, but in all cases the birds fled away before the male gibbon could catch it. In three cases the bird were ducks and in one case it was a

28. Romp bite (RB)

Two, sometimes even three animals romp, wrestle, bite lightly and let out now and then flute sounds. Romp bite can be carried out in different forms. The animals are situated on the ground of the island. One animal is holding himself with the hands on a branch or rope, the other animal is hanging on the legs of the first one and gets pulled up through the legs of the first one and leads to the mouth (adult with infant). Both animals can also be hanging upside down and only hold themselves with their legs on a branch or rope. This interaction occurs mainly with arms and mouth.

Function: Play behaviour

Comment: Mostly the male and infant were playing together while the female was observing them from a distance. They were mostly playing while hanging on a branch or sitting in the hammock.

29. Quick chase (play) (QCp)

An animal stalks his play partner over the island, respectively chases it over a longer distance. After a short break or temporary *Romp bite* (27) the hunt can be continued 'with the tables turned'. Quick chase can happen on the ground of the island as well as in the higher situated area. Integrated are mostly *bipedal walk* (14), *brachiation* (10) and *jump* (08).

Function: Play behavior

Comment: If the infant and the male were playing together, they sometimes would chase each other quickly in a playful way. In most cases the male was chasing the infant.

30. Quick chase (aggressive) (QSa)

Like with *Quick chase play*, an animal stalks another animal over the island, respectively chases it over a longer distance. The vigorous, high-speed pursuit of one individual by another is commonly unidirectional. Such pursuit rarely lasts more than a few seconds, but many yards may be covered very swiftly. The lead individual selects a route partly in accordance with the movements of the pursuing individual, who may follow this route but is more likely to attempt interception by cutting corners and reducing distance wherever possible. While trying to elude the second individual, the lead one may *grimace* and/or *squeal*, and sometimes other observing individuals make loud *whoop* sounds. If successful in catching up, the pursuer may grapple and bite the other.

Comment: In the case if the male was playing to rough with the infant and the infant began to scream a bit, the female started to chase the male in an aggressive way immediately until the male was far away from the infant.

31. Push oneself between two animals (PA)

Adult animals are in a copulation position. The infant pushes oneself between both animals and takes by opportunity a *nipple in the mouth* (01)

Function: Avoiding beget another animal, which will push aside the infant out of his position or learn the mating behavior.

32. Observe (Ob)

The animal can be in any given position. Besides the surrounding gets searched visual or at least observed attentive.

Function: Observe the surrounding, territorial behavior

33. Reprimand the animal (RA)

Touch or bite in the neck of another animal with slightly opened mouth, or pushes the other animal away with the hand.

Function: Protest against a behavior pattern of one of the same species.

34. Threat bite (TB)

The animal opens the mouth, shows its teeth and snaps at or bites in the air directed to the animal, which this action is directed to.

Function: Directed treat against an animal of the same species.

35. Threaten (Th)

An animal stares with half opened mouth at an animal of the same species, or both animals sit or stand opposite each other and threaten each other. Threaten can also be against different species.

Function: Directed threat.

5. Impress behaviour

36. Wild impress swing (WS)

Behaviour pattern which is always shown by females during duet vocalization. Males against that show this behaviour pattern as a reaction to disturbing factors. The animal shows a quick series of brachiating elements, which can be interrupted for a short period of time by *Jump* (08). With this behavior element the proportionately is small and is limited to one tree, never the whole island or more trees are being used.

Function: Impress behavior, play behavior

37. Pirouette (Pi)

The animal spins round his own axis. This can take place slowly out of *walk bipedal* (14), a quick *bipedal walk* (14), or from a stationary position (sitting).

Function: Impress behavior, draw attention to oneself.

6. Food supply

38. Grab grass (GG)

An animal grabs in the grass, pulls out a truss, inspects the catch, and eats the grass or small organism, which is situated in the grass. The rest will be dropped again.

Function: Food intake

39. Catch food (CF)

The animal catches food ingredients, like fruit and vegetables, which is thrown onto the island by the animal keeper or visitors.

Function: Guarantee the food

40. Catch insects (CI)

The animal moves his hand slowly to the side of the insect and grabs it then quick as lightning. By slowly opening the fist the catch is being inspected.

Function: Catch food.

41. Transport food (TF)

Separated food pieces are being transported by the hand, foot or mouth (infants). In cohesion with food transport combined locomotion forms can occur.

Function: Guarantee the food

Comment: If the animal did not catch the food (which was thrown by the animal keeper onto the island), the food fell on the ground. Then both the male and female would grab the food from the ground and transport it in hand, feet or mouth to another place to eat it.

42. Taste food (TF)

The animal tastes the food piece, while it scents it, licks off or tastes a small piece

Function: Diagnose the enjoy ability or quality of the food.

Comment: During filming it was once observed that the female grabbed clay and tasted it. But she did not like the taste and threw it away.

43. Remove food (RF)

An animal is trying to grab food from the mouth, hand or foot from another animal. Besides only pieces are being broken off, it seldom results in complete food loss for an animal. If this action takes place between an adult and infant, the adult allows the infant to do it. If it occurs between two adults it can result in threat signs.

Function: Food consume.

Comment: This behaviour only occurred between the female and the infant. The infant tried once to remove food from the male, but the male did not allow it.

44. Grab food (GF)

The animal inspects the food, which lies on the island and grabs food parts.

Function: Directed choice of food.

Comment: There is hanging one ball high in the tree on the island where once in a while the animal keeper is putting food in just before the animals are being released onto the island. The animals grab the food out of this ball. When the male or female can not catch the food which is thrown onto the island by the animal keeper, they will grab the food from the ground.

45. Soak bread (SB)

The animal takes hold of a slice of bread and transports it to the edge of the island. The bread slice is being laid in the water and taken out and consumed after various intervals.

Function: Soak the food.

Comment: The gibbons in Apenheul were never fed bread, so they could not perform this behaviour.

46. Lick off vegetation (LV)

The object (branch) is being licked off by the animal.

Function: Food consumes, ?.

Comment: During the whole observation period at Apenheul it had never rained. This may be reason that this behaviour was not observed.

47. Bite off vegetation (BV)

Leaves, branches and rind are being bitten off by the animal. Leaves serve as food, rarely it is used as a play object. Branches are being bitten off, to be used as a play object. Rinds are being bitten off to search for insects, which can be situated underneath.

Function: Food consume, play behavior.

48. Break off vegetation (BrV)

The animal is situated in the tree, in the bushes or in front of a bush and breaks off leaves or buds, which serves as food. The animal can also break off a small branch to be used as a play object.

Function: Food consume, play behavior.

49. Lick off water-drops (LW)

An animal licks off drops of water from object or from his body (after rain).

Function: Liquid consume, body maintenance.

Comment: During the whole observation period at Apenheul it had never rained. Only once the male licked off drops of water from his leg after he put his leg into the water.

7. Food consume

50. Drink (Dr)

The animal bends down to the water surface and leads the water with the tongue in the mouth, or the hand is being hold in the water and then drinks from the cavity of the hand, or the water is being licked off from the fur of the back of the hand.

Function: Liquid consume.

Comment: Both the male and female drink water out of the ditch with their mouth or hand while hanging on a tree or sitting on the bridge.

51. Eat (Ea)

The food is being brought to the mouth of the animal with a limb and bitten off. The animal is holding the food with the foot or the hand and bites off, or both hands or feet are holding the food and brings it to the mouth, or the food is being hold with the foot and broken off with the hand, or one hand holds the food and the other hand brings the food to the mouth.

Function: Food consume.

8. Excretion

52. Urinate (Ur)

During urinating the animal is situated on a standpoint, which is situated higher then the ground of the island or the surface of the water. Besides various positions can be taken: (1) An animal is hanging with both hands on a branch and urinates. (2) The animal is holding on itself with both hands on a branch, the feet are standing on a further branch, and the upper part of the body is inclined forward. (3) The animal is situated on a plank bridge and urinates standing or seated in the water.

Function: Excretion

53. Defecate (De)

Body posture and standard are identical with *Urinate* (50).

Function: Excretion

9. Rest behaviour

54. Rest (Re)

The animal sits or lies and takes a rest. By sunbathing the animal lies on his back, stretches all limbs or crosses the arms at the backside of the head with the body placed in the sun.

Function: Rest

55. Doze (Do)

The animal is laying or sitting on the ground or on a branch. The attention is reduced, the eyes are temporary closed. Besides, the animal is lying on its back, with arms and legs stretched out. Or the animal is lying on its side, a hand under the head; the other arm is lying on the body or sidelong. When seated dozen the animal is cowered, the head is bent forward.

Function: Rest

56. Sleep (SI)

The animal sleeps in the identical body posture like with *Doze* (52).

Function: Sleep

10. Intragroup behaviour

57. Body contact (BC)

Two or more animals are sitting close to each other and have body contact. Now and then allogrooming occurs.

Function: Exchange of warmth by body contact. Demonstration or mutual assurance of a close social relation.

58. Embrace (Em)

An animal embraces the body of another animal with his arms. This behavior pattern takes mostly place between infants and their mother. In contrast with body contact this gesture is however not being answered.

Function: Structure of bodily vicinity of another animal.

59. Invite for social grooming (ISG)

An animal presents itself to another animal by presenting a part of the body, which will be groomed. First an animal grooms another animal for a short while and presents then a part of its own body.

Function: Urge for social grooming.

60. Allogrooming (AG)

Divide and search for dirtiness and skin scales in the fur. The fur is being combed through by the fingers, and the dirtiness is being licked off, comprised by lips, comprised by teeth and grabbed with fingers.

Function: Fur care, gesture of reconciliation, pair bond behaviour.

11. Comfort behaviour

61. Lick off finger (LF)

A finger or more fingers together are being put in the mouth and licked off or the finger(s) are licked off outside the mouth.

Function: Clean the finger.

Comment: The female always licked off her fingers during and after she was urinating.

62. Lick off arm (LA)

The animal licks off its own arm.

Function: Clean the arm.

63. Body shake (Bs)

The animal is standing or sitting, lays the head in the neck, places the arms sidelong the body and holds them slightly up, the hands are bent down in a hook shape. The animal shakes the whole body, which can be followed by wave movements from the head to the hands. The teeth are being bared during this occurrence.

Function: Remove water-drops or dirtiness from the fur, stretch behaviour.

64. Scratch (Sc)

The animal is scratching itself with the hand or foot. The individual draws the fingertips, fingers partly curled and held together in claw like fashion, along some surface of the torso or limb.

Function: Body care.

65. Stretch (St)

The animal stretches its whole body and spreads all limbs or the limbs one by one wide from the body, strains its muscles and relaxes again.

Function: Stretch occurrence.

66. Shake out the hand (SH)

The animal shakes a hand, in which it held an object before or is still holding it. The impulse comes from the underarm.

Function: Remove objects or dirtiness.

67. Autogrooming (AuG)

Identical behaviour course as with *Allogrooming* (57). The animal carries out the procedure on its own body.

Function: Body care.

68. Pull out hair/skin (PH)

Hair- or skin scales is being pulled out by the animal itself. This behavior pattern arises by preference in optical reach and can indicate that it is caused by dirt.

Function: Body care

69. Clean fingernail (CF)

The animal uses the fingernail of its forefinger of one hand, to clean the nails of the other hand.

Function: Body care

70. Rub the nose (RN)

The animal rubs its nose with the backside or inside of the hand.

Function: Hinder itch irritation.

71. Yawn (Ya)

The mouth is opened wide, exposing the upper and lower teeth and sometimes the gums as well. The head may be thrown far back

Function: Tiredness symptom, boredom

72. Sneeze (Sn)

Intense emission of air through the nose.

Function: Protecting reflex on chemical, thermal or mechanical stimulation of the nose mucous membrane

13. Sexual behaviour

73. Penis manipulation

The male sits with its legs spread and touches its penis with shaking hand movements. At times the hand is being leaded to the mouth and scented. An ejaculation could not be observed. This behaviour occurs in a relaxed situation.

74. Invite for anogenital inspection (IAI)

The animal stands or sits on the ground and raises up its behind, so that the anogenital area becomes accessible.

Function: Invitation for anogenital inspection.

75. Anogenital inspection (AI)

The animal lays or sits behind the social partner, bents forward and scents, licks or touches the anogenital area. If the hand is being used, then the animal licks or scents this hand.

Function: Sexual disposal of the female is being checked.

76. Copulation (Co)

The male approaches the female from behind, which has bended the upper part of the body forward, or bends the upper part of the body forward with body contact. During the copulation no other behavior parameter can be observed, because the copulation on account of the *Mating interfering* (29) the infant always in very short time makes great demands.

Function: Multiply.

77. Refuse copulation (RC)

The female is refusing the *copulation* (72), while she moves herself away from the male.

Function: Refuse copulation

14. Acoustic communication

78. Acoustic communication (AC)

Function: Emphasise a role in territorial advertisement, mate attraction and maintenance of pair and family bonds.

15. Stationary posture

79. Stand

The body is supported on a substratum, all or most of the weight being on one to three appendages: two legs provide the main support, but one arm and hand may act as stabilizer with fingertips touching the substratum or hooked on an overhead structure. The back rarely shows curvature. The soles either lie flat, with the great toe splayed outward, or grip the substratum. The arms may be held below, at, or above shoulder level; when not used to assist in support or suspension, the arms are commonly between thigh and shoulder level, with wrists limb and forearms akimbo.

80. Sit

The body is supported on a substratum or wedged among several structures, all or most of the weight being on the ischial callosities. The torso may be propped against a framework of structures. The back can be straight or curved, depending mainly on the degree of relaxation, and the head held upright or the chin rested against the chest, knees or wrists. The legs may be extended and used as braces against other supports, or flexed with the thighs sometimes up against the abdomen and chest, thereby propping the torso on a tripod of contact points. The arms are often folded, hugging the flexed knees to the chest, or the forearms may rest on the thighs or knees.

81. Lie

The body is supported on a substratum, all or most of the weight being on the torso, which is extended along or draped over a supporting structure. The arms and/or legs may be in various positions, folded close to the torso or fully extended, limb or propped against supports. When the individual is on a stable substratum the hands and/or feet are relaxed and the digits partly curled, but adjacent structures may be

gripped for added stability when the supports are flimsy or in motion. The head may simply loll freely or rest on the forearms, hands, or substratum.

83. Jerky body movements

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Appendix 2: Individual Distances

Distance of every animal set apart in absolute numbers and in percentages.

Dyad ¹	Distance class ²								Total	
	1		2		3		4			
Apeldoorn										
F - M	108	10.7%	94	9.3%	154	15.3%	652	64.7%	1008	100%
F - I	389	38.6%	197	19.5%	251	24.9%	171	17.0%	1008	100%
M - I	133	13.2%	67	6.6%	174	17.3%	634	62.9%	1008	100%
Amsterdam										
F - M	15	8.9%	35	20.8%	34	20.3%	84	50.0%	168	100%
Beekse Bergen										
F - M	15	6.4%	50	21.4%	89	38.0%	80	34.2%	234	100%
F - I	81	34.6%	68	29.0%	50	21.4%	35	15.0%	234	100%
M - I	19	8.1%	65	27.8%	84	35.9%	66	28.2%	234	100%
Hannover 1										
F - M	7	3.4%	61	29.9%	84	41.2%	52	25.5%	204	100%
F - I	107	52.5%	50	24.5%	31	15.2%	16	7.8%	204	100%
M - I	9	4.4%	58	28.4%	84	41.2%	53	26.0%	204	100%
Hannover 2										
F - M	3	1.7%	28	15.5%	39	21.7%	110	61.1%	180	100%
F - I	89	49.5%	33	18.3%	24	13.3%	34	18.9%	180	100%
F -S	30	16.7%	68	37.8%	47	26.1%	35	19.4%	180	100%
M - I	0	0.0%	28	15.6%	44	26.1%	108	19.4%	180	100%
M - S	0	0.0%	19	10.6%	49	27.2%	112	62.2%	180	100%
I - S	31	17.2%	79	43.9%	42	23.3%	28	15.6%	180	100%

¹ Abbreviations: F = Female, M = Male, I = Infant.

² Distance classes: 1 = Body contact, 2 = 0.1 – 1m, 3 = 1.1 – 3m, 4 = > 3m.

Appendix 3: Absolute Frequencies

Absolute frequencies of the researched behaviour elements of the white-cheeked crested gibbon group of Apeldoorn.

Number	Behaviour element	Female	Male	Infant
1	Take nipple in mouth	0	0	489
2	Belly carrying	11	0	11
3	Bring in the infant	3	0	0
4	Reprimand the infant	1	0	0
5	Swing/hang	184	208	201
6	Make a tumble	0	5	0
7	Somersault	0	2	0
8	Jump	27	98	444
9	Climb	190	250	668
10	Brachiate	399	645	907
11	Free fall	3	20	97
12	Tumble around the rope	0	0	2
13	Cower	113	145	277
14	Swing on one arm	57	86	278
15	Walk bipedal	60	201	353
16	Sliding down rope/branch	0	4	2
17	Explorative grab at objects	4	14	9
18	Research object	0	4	3
19	Bite in object	0	14	37
20	Get the object out of the water	1	5	1
21	Throw up and catch the object	0	0	17
22	Throw away/up the object	0	2	8
23	Object play rope/stick	0	5	75
24	Play with grass	0	2	2
25	To lay about the object	0	0	0
26	Inhibited bite	0	2	0
27	Grab at social partner	2	2	3
28	Grab at bird	0	4	0
29	Romp bite	23	256	258
30	Quick chase play	5	35	16
31	Quick chase aggressive	6	2	0
32	Push oneself between 2 animals	0	0	6
33	Observe	144	199	81
34	Reprimand the animal	2	0	0
35	Threat bite	0	2	0
36	Threaten	0	1	0
37	Wild impress	7	1	1
38	Pirouette	0	0	4
39	Grab grass	1	0	0
40	Catch food	12	7	0
41	Catch insect	34	30	21
42	Transport food	7	8	2
43	Taste food	0	0	0

Appendix 3. Continued.

Number	Behaviour element	Female	Male	Infant
44	Remove food	0	0	19
45	Grab food	20	15	8
46	Soak bread	0	0	0
47	Lick if vegetation	0	0	0
48	Bite of vegetation	18	28	52
49	Break off vegetation	115	206	182
50	Lick off water-drops	0	0	0
51	Drink	5	7	6
52	Eat	187	269	259
53	Urinate	10	5	1
54	Defecate	7	4	2
55	Rest	34	27	1
56	Doze	16	0	0
57	Sleep	0	0	0
58	Body contact	475	46	489
59	Embrace	7	2	1
60	Invite for social grooming	3	7	6
61	Allogrooming	110	62	77
62	Lick off finger	51	20	12
63	Lick off arm	0	0	2
64	Body shake	1	9	0
65	Scratch	195	430	329
66	Stretch	0	7	0
67	Shake out hand	0	3	0
68	Autogrooming	11	5	0
69	Pull out hair/skin	0	0	0
70	Clean fingernail	0	2	0
71	Rub the nose	6	5	2
72	Yawn	9	20	1
73	Sneeze	1	9	1
74	Penis manipulation	0	1	0
75	Invite for anogenital inspection	10	0	0
76	Anogenital inspection	4	3	0
77	Copulation	27	15	0
78	Refuse copulation	1	0	0
79	Vocalization	23	18	2
80	Stand	25	15	3
81	Sit	371	538	210
82	Lie	15	42	9
83	Jerky body movements	70	0	0

Appendix 4: Comparison between Male and Female

Statistic comparison of the frequencies of each behaviour element between male and female of the study pair.

Number	Behaviour element	Male	Female	F - M	F - M
1	Take nipple in mouth	0	0	n.t.	n.t.
2	Belly carrying	0	11	0,001	0,001
3	Bring in the infant	0	3	0,083	n.s.
4	Reprimand the infant	0	1	n.t.	n.t.
5	Swing/hang	208	184	0,225	n.s.
6	Make a tumble	5	0	0,025	< 0,05
7	Somersault	2	0	0,157	n.t.
8	Jump	98	27	0	< 0,001
9	Climb	250	190	0,004	< 0,01
10	Brachiation	645	399	0	< 0,001
11	Free fall	20	3	0	< 0,001
12	Tumble around the rope	7	2	0,096	n.s.
13	Cower	145	113	0,046	< 0,05
14	Swing on one arm	86	57	0,015	< 0,05
15	Walk bipedal	201	60	0	< 0,001
16	Sliding down rope/branch	2	0	n.t.	n.t.
17	Explorative grab at objects	14	4	0,018	< 0,05
18	Research object	4	0	0,046	n.t.
19	Bite in object	14	0	0	< 0,001
20	Get the object out of the water	5	1	n.t.	n.t.
21	Throw up and catch the object	0	0	n.t.	n.t.
22	Throw away/up the object	2	0	n.t.	n.t.
23	Object play rope/stick	5	0	n.t.	n.t.
24	Play with grass	2	0	n.t.	n.t.
25	To lay about the object	0	0	n.t.	n.t.
26	Inhibited bite	2	0	n.t.	n.t.
27	Grab at social partner	2	2	n.t.	n.t.
28	Grab at bird	4	0	n.t.	n.t.
29	Romp bite	256	23	0	< 0,001
30	Quick chase play	35	5	0	< 0,001
31	Quick chase aggressive	2	6	0.157	n.s.
32	Push oneself between 2 animals	0	0	n.t.	n.t.
33	Observe	199	144	0,003	< 0,01
34	Reprimand the animal	0	2	n.t.	n.t.
35	Threat bite	2	0	n.t.	n.t.
36	Threaten	1	0	n.t.	n.t.
37	Wild impress	1	7	0	< 0,001
38	Pirouette	0	0	n.t.	n.t.
39	Grab grass	0	1	n.t.	n.t.
40	Catch food	7	12	0,251	n.s.
41	Catch insect	30	34	0,617	n.s.
42	Transport food	8	7	0,796	n.s.
43	Taste food	0	0	n.t.	n.t.
44	Remove food	0	0	n.t.	n.t.

Appendix 4. Continued.

Number	Behaviour element	Male	Female	F - M	F - M
45	Grab food	15	20	0,398	n.s.
46	Soak bread	0	0	n.t.	n.t.
47	Lick if vegetation	0	0	n.t.	n.t.
48	Bite of vegetation	28	18	0,14	n.s.
49	Break off vegetation	206	115	0	< 0,001
50	Lick off water-drops	0	0	n.t.	n.t.
51	Drink	7	5	0,564	n.s.
52	Eat	269	187	0	< 0,001
53	Urinate	5	10	0,197	n.s.
54	Defecate	4	7	0,366	n.s.
55	Rest	27	34	0,37	n.s.
56	Doze	0	16	0	< 0,001
57	Sleep	0	0	n.t.	n.t.
58	Body contact	46	475	0	< 0,001
59	Embrace	2	7	0,096	n.s.
60	Invite for social grooming	7	3	0,206	n.s.
61	Allogrooming	62	110	0	< 0,001
62	Lick off finger	20	51	0	< 0,001
63	Lick off arm	0	0	n.t.	n.t.
64	Body shake	9	1	0,011	< 0,05
65	Scratch	430	195	0	< 0,001
66	Stretch	7	0	0,008	< 0,01
67	Shake out hand	3	0	n.t.	n.t.
68	Autogrooming	5	11	0,134	n.s.
69	Pull out hair/skin	0	0	n.t.	n.t.
70	Clean fingernail	2	0	n.t.	n.t.
71	Rub the nose	5	6	0,763	n.s.
72	Yawn	20	9	0,041	< 0,05
73	Sneeze	9	1	0,011	< 0,05
74	Penis manipulation	1	0	n.t.	n.t.
75	Invite for anogenital inspection	0	10	0,002	< 0,05
76	Anogenital inspection	3	4	0,705	n.s.
77	Copulation	15	27	n.t.	n.t.
78	Refuse copulation	0	1	n.t.	n.t.
79	Vocalization	18	23	0,435	n.s.
80	Stand	15	25	0,114	n.s.
81	Sit	538	371	0	< 0,001
82	Lie	42	15	0	< 0,001
83	Jerky body movements	0	70	0	< 0,001

The behaviour elements written **bold** are highly significant ($p < 0.001$).

Appendix 5: Comparison between Adults and Infant

a) Statistical comparison of the behavioural frequencies between male and infant.

Number	Behaviour	Absolute frequency		Significance value	
		Male	Infant	Male - Infant	
1	Take nipple in mouth	0	489	< 0,001	0
2	Belly carrying	0	11	0,001	0,001
3	Bring in the infant	0	0	n.t.	n.t.
4	Reprimand the infant	0	0	n.t.	n.t.
5	Swing/hang	208	201	n.s.	0,729
6	Make a tumble	5	0	n.t.	n.t.
7	Somersault	2	0	n.t.	n.t.
8	Jump	98	444	< 0,001	0
9	Climb	250	668	< 0,001	0
10	Brachiate	645	907	< 0,001	0
11	Free fall	20	97	< 0,001	0
12	Tumble around the rope	7	17	< 0,05	0,041
13	Cower	145	277	< 0,001	0
14	Swing on one arm	86	278	< 0,001	0
15	Walk bipedal	201	353	< 0,001	0
16	Sliding down rope/branch	4	2	n.t.	n.t.
17	Explorative grab at objects	14	9	n.s.	0,297
18	Research object	4	3	n.s.	0,705
19	Bite in object	14	37	0,001	0,001
20	Get the object out of the water	5	1	n.s.	0,102
21	Throw up and catch the object	0	17	< 0,001	0
22	Throw away/up the object	2	8	n.s.	0,058
23	Object play rope/stick	5	75	< 0,001	0
24	Play with grass	2	2	n.t.	n.t.
25	To lay about the object	0	0	n.t.	n.t.
26	Inhibited bite	2	0	n.t.	n.t.
27	Grab at social partner	2	3	n.t.	n.t.
28	Grab at bird	4	0	n.t.	n.t.
29	Romp bite	256	258	n.s.	0,93
30	Quick chase play	35	16	n.s.	0,08
31	Quick chase aggressive	2	0	n.t.	n.t.
32	Push oneself between 2 animals	0	6	< 0,05	0,014
33	Observe	199	81	< 0,001	0
34	Reprimand the animal	0	0	n.t.	n.t.
35	Threat bite	2	0	n.t.	n.t.
36	Threaten	1	0	n.t.	n.t.
37	Wild impress	1	1	n.t.	n.t.
38	Pirouette	0	4	n.t.	n.t.
39	Grab grass	0	0	n.t.	n.t.
40	Catch food	7	0	< 0,01	0,008
41	Catch insect	30	21	n.s.	0,208
42	Transport food	8	2	n.s.	0,058
43	Taste food	0	0	n.t.	n.t.

Appendix 5. Continued.

Number	Behaviour	Absolute frequency		Significance value	
		Male	Infant	Male-Infant	
44	Remove food	0	19	< 0,001	0
45	Grab food	15	8	n.s.	0,144
46	Soak bread	0	0	n.t.	n.t.
47	Lick if vegetation	0	0	n.t.	n.t.
48	Bite of vegetation	28	52	< 0,01	0,007
49	Break off vegetation	206	182	n.s.	0,223
50	Lick off water-drops	0	0	n.t.	n.t.
51	Drink	7	6	n.s.	0,782
52	Eat	269	259	n.s.	0,663
53	Urinate	5	1	n.s.	0,102
54	Defecate	4	2	n.s.	0,414
55	Rest	27	1	< 0,001	0
56	Doze	0	0	n.t.	n.t.
57	Sleep	0	0	n.t.	n.t.
58	Body contact	46	489	< 0,001	0
59	Embrace	2	1	n.t.	n.t.
60	Invite for social grooming	7	6	n.s.	0,782
61	Allogrooming	62	77	n.s.	0,203
62	Lick off finger	20	12	n.s.	0,157
63	Lick off arm	0	2	n.t.	n.t.
64	Body shake	9	0	< 0,01	0,003
65	Scratch	430	329	< 0,001	0
66	Stretch	7	0	< 0,01	0,008
67	Shake out hand	3	0	n.t.	n.t.
68	Autogrooming	5	0	n.t.	n.t.
69	Pull out hair/skin	0	0	n.t.	n.t.
70	Clean fingernail	2	0	n.t.	n.t.
71	Rub the nose	5	2	n.s.	0,257
72	Yawn	20	1	< 0,001	0
73	Sneeze	9	1	< 0,05	0,011
74	Penis manipulation	1	0	n.t.	n.t.
75	Invite for anogenital inspection	0	0	n.t.	n.t.
76	Anogenital inspection	3	0	n.t.	n.t.
77	Copulation	15	0	< 0,001	0
78	Refuse copulation	0	0	n.t.	n.t.
79	Vocalization	18	2	< 0,001	0
80	Stand	15	3	< 0,01	0,005
81	Sit	538	210	< 0,001	0
82	Lie	42	9	< 0,001	0
83	Jerky body movements	0	0	n.t.	n.t.

Behavioural elements written in **bold** are highly significant ($p < 0.001$).

Appendix 5. Continued.

b) Statistic comparison of the behaviour frequencies between female and infant.

Number	Behaviour	Absolute frequency		Significance value	
		Female	Infant	Female - Infant	
1	Take nipple in mouth	0	489	< 0,001	0
2	Belly carrying	11	11	n.s.	1
3	Bring in the infant	3	0	n.t.	n.t.
4	Reprimand the infant	1	0	n.t.	n.t.
5	Swing/hang	184	201	n.s.	0,386
6	Make a tumble	0	0	n.t.	n.t.
7	Somersault	0	0	n.t.	n.t.
8	Jump	27	444	< 0,001	0
9	Climb	190	668	< 0,001	0
10	Brachiate	399	907	< 0,001	0
11	Free fall	3	97	< 0,001	0
12	Tumble around the rope	2	17	0,001	0,001
13	Cower	113	277	< 0,001	0
14	Swing on one arm	57	278	< 0,001	0
15	Walk bipedal	60	353	< 0,001	0
16	Sliding down rope/branch	0	4	n.t.	n.t.
17	Explorative grab at objects	4	9	n.s.	0,166
18	Research object	0	3	n.t.	n.t.
19	Bite in object	0	37	< 0,001	0
20	Get the object out of the water	1	1	n.t.	n.t.
21	Throw up and catch the object	0	17	< 0,001	0
22	Throw away/up the object	0	8	< 0,05	0,005
23	Object play rope/stick	0	75	< 0,001	0
24	Play with grass	0	2	n.t.	n.t.
25	To lay about the object	0	0	n.t.	n.t.
26	Inhibited bite	0	0	n.t.	n.t.
27	Grab at social partner	2	3	n.t.	n.t.
28	Grab at bird	0	0	n.t.	n.t.
29	Romp bite	23	258	< 0,001	0
30	Quick chase play	5	16	< 0,05	0,016
31	Quick chase aggressive	6	0	< 0,05	0,014
32	Push oneself between 2 animals	0	6	< 0,05	0,014
33	Observe	144	81	< 0,001	0
34	Reprimand the animal	2	0	n.t.	n.t.
35	Threat bite	0	0	n.t.	n.t.
36	Threaten	0	0	n.t.	n.t.
37	Wild impress	7	1	< 0,05	0,034
38	Pirouette	0	4	n.t.	n.t.
39	Grab grass	1	0	n.t.	n.t.
40	Catch food	12	0	0,001	0,001
41	Catch insect	34	21	n.s.	0,08
42	Transport food	7	2	n.s.	0,096
43	Taste food	0	0	n.t.	n.t.

Appendix 5. Continued.

Number	Behaviour	Absolute frequency		Significance value	
		Female	Infant	Female - Infant	
44	Remove food	0	19	< 0,001	0
45	Grab food	20	8	< 0,05	0,023
46	Soak bread	0	0	n.t.	n.t.
47	Lick if vegetation	0	0	n.t.	n.t.
48	Bite of vegetation	18	52	< 0,001	0
49	Break off vegetation	115	182	n.t.	n.t.
50	Lick off water-drops	0	0	< 0,001	0
51	Drink	5	6	n.s.	0,763
52	Eat	187	259	0,001	0,001
53	Urinate	10	1	< 0,05	0,007
54	Defecate	7	2	n.s.	0,096
55	Rest	34	1	< 0,001	0
56	Doze	16	0	n.t.	n.t.
57	Sleep	0	0	n.t.	n.t.
58	Body contact	475	489	n.s.	0,652
59	Embrace	7	1	< 0,05	0,034
60	Invite for social grooming	3	6	n.s.	0,317
61	Allogrooming	110	77	< 0,05	0,016
62	Lick off finger	51	12	< 0,001	0
63	Lick off arm	0	2	n.t.	n.t.
64	Body shake	1	0	n.t.	n.t.
65	Scratch	195	329	< 0,001	0
66	Stretch	0	0	n.t.	n.t.
67	Shake out hand	0	0	n.t.	n.t.
68	Autogrooming	11	0	0,001	0,001
69	Pull out hair/skin	0	0	n.t.	n.t.
70	Clean fingernail	0	0	n.t.	n.t.
71	Rub the nose	6	2	n.s.	0,157
72	Yawn	9	1	< 0,05	0,011
73	Sneeze	1	1	n.t.	n.t.
74	Penis manipulation	0	0	n.t.	n.t.
75	Invite for anogenital inspection	10	0	< 0,05	0,002
76	Anogenital inspection	4	0	n.t.	n.t.
77	Copulation	27	0	< 0,001	0
78	Refuse copulation	1	0	n.t.	n.t.
79	Vocalization	23	2	< 0,001	0
80	Stand	25	3	< 0,001	0
81	Sit	371	210	< 0,001	0
82	Lie	15	9	n.s.	0,221
83	Jerky body movements	70	0	< 0,001	0

Behavioural elements written in **bold** are highly significant ($p < 0.001$).

Appendix 6: Ethograms of Siamang and White-Cheeked Crested Gibbon compared

For each behavioural element mentioned in the siamang ethogram (Orgeldinger, 1999), the table indicates if it is represented in the white-cheeked crested gibbon ethogram of this study.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
Take care of young		
1	Take nipple	–
2	Comfort suck	–
3	Quick nipple change	/
4	Suck	+
5	Refuse nipple contact	–
6	Remove young from nipple	–
7	Look after young	–
8	Positionize young	–
9	Hold up the young	–
10	Carry the young on the hand	–
11	Back carrying	–
12	Belly carrying	++
13	Protect the young	–
14	Bring in the young	++
15	Ritualised neck bite	–
16	Leaving sounds	–
Play behaviour		
17	Swing	+
18	Slide on the ground	–
19	Make a tumble	++
20	Salto	++
21	Do gymnastics on a bar	+?
22	Turn a pirouette	+
23	Blind stump	–
24	Hit on the head	–
25	Explorative grab at object	++
26	Grab swollen throat sack	–
27	Playful bite in object	++
28	Head shake with object	–
29	Carefully touch an object	–
30	Quickly bump against an object	–
31	Jump over a play object	–
32	Fling away a play object	++

Appendix 6. Continued.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
33	Catch a play object	++
34	Shake sound making play object	–
35	Swing with play object	–
36	To hit with an object	–
37	Push itself flat on the ground	–
38	Lie on the back	–
39	Quick body movements	?
40	Quick touch	–
41	To hit in blank	–
42	Climb on a social partner	/
43	Playful hit	/
44	Hit with an object	–
45	Jump playfull	/
46	Inhibited bite	+
47	Pull a partner	–
48	Hold fast	/
49	Push away	–
50	Romp bite	++
51	Playful chase	++
52	Make contact through window	–
53	Make contact with animal keeper	–
54	Tense grin	–
55	Playful threat	–
56	Playface	–
57	Playsound	–
Intergroup behaviour		
58	Invite for look around	–
59	Slow chase	–
60	Quick body movements	?
61	Raise the head	–
62	Ritualized neck bite	–
63	Shake social partner	–
64	Invite for hit	/
65	Be together	–
66	Touch quickly	–
67	Lay on hand	–
68	Hold hand	–
69	Caress	–
70	Embrace	+
71	Body contact	++
72	Invite for social grooming	++

Appendix 6. Continued.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
73	Allogrooming	++
74	Eat from fur of a partner	—
75	lick off partner	—
76	Milk	—
77	Not directed threat	—
78	Directed threat	++
79	Threat bite	++
80	Mouth to mouth threat	—
81	Bite threat	—
82	Hold threatening	—
83	Genital threat	—
84	Push between	+
85	Bounce aggressive	—
86	Jump aggressive	—
87	Hit aggressive	—
88	Chase aggressive	+
89	Bite	—
90	Bite struggle	—
91	Injure bite	—
92	Jealous disturb	++
93	Couple disturb	+
94	Make up an conflict	—
95	Avoid	—
96	Leaving sound	—
97	Sholder response	—
98	Tense grin	—
99	Fear face	—
100	Fear urinate	—
101	Fear tremble	—
102	Beg	—
103	Slow chase	—
104	Snatch away food	—
105	Passive food sharing	+
106	Active food sharing	—
107	Prepare food pieces	—
108	Passive fluit sharing	—

Appendix 6. Continued.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
Territorial behaviour		
109	Quarantee	—
110	Tense grin	—
111	Excited croak	—
112	Set up fur	—
113	Stereotypical swing or brachiation	—
114	Bipedal run	—
115	Swing and throw away objects aggressive	—
116	Shake sound making impress objects	—
117	Shade boxing	—
118	Impress pirouette	+
119	<i>Tridimensional impressveranstaltung</i>	—
120	Stare at	—
121	<i>Durch wegschauewn unterbrochenes Anstarren</i>	—
122	Turn back upon	—
123	Nod one's head threatening	—
124	Excited bodywhip	—
125	Undirected threatbite	++
126	Theat bite	++
127	Aggressive object bite	—
128	Alarm sound	—
129	Alarm call	—
130	Duetsong	+
131	Jump aggressive on seperation wall	—
132	Quick attack	—
Sexual behaviour		
133	Invite for genital inspection	+
134	Anogenital inspection	++
135	Penis erection	—
136	Penis manipulation	++
137	Oral stimulation of the penis by female	—
138	Oral stimulation of the female genitalien by male	—
139	Female copulation invitation (present genital)	—
140	Male copulation invitation	—
141	Copulation request	—
142	Copulation	++
143	Copulation face	—
144	Copulation sound	—
145	Refuse copulation	+
146	Slow chase	—

Appendix 6. Continued.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
Comfort behaviour		
147	Scratch	++
148	Scour the skin	–
149	Body shake	++
150	Shake hand	++
151	Take own bodypart in mouth	–
152	Autogrooming	++
153	Lick off own bodypart	+
154	Move tongue to and fro	–
155	Pull out hair/scale	++
156	Clean fingernail	++
157	Chew on fingernail	–
158	Rub the nose	++
159	Pick one's nose	–
160	Anogenital inspection on oneself	–
161	Yawn	++
162	Stretch	++
Rest and sleep behaviour		
163	Observe	++
164	Rest	++
165	Doze	++
166	Sleep	++
Position posture		
167	Hang	++
168	Stand	++
169	Cower	+
170	Sit	++
171	Lie	++
Locomotion behaviour		
172	Brachiate	++
173	Bipedal walk	++
174	Tripedal walk	–
175	Quadruple walk	–
176	Quadruple lame walk	–
177	Old age lame walk	–
178	Climb	++
179	Jump	++
180	Free fall	++

Appendix 6. Continued.

Element Nr.	Behavioural element of siamang ethogram	White-cheeked crested gibbon ethogram
Food and liquid supply		
181	Excited croak	—
182	Niggle for food	—
183	Catch insect	++
184	Transport food	++
185	Taste food	++
186	Eat	++
187	Squeeze fruit	—
188	Crumble food	—
189	Lick off water-drops	++
190	Drink	++
Excretion		
191	Urinate	++
192	Defecate	++

Symbols: ++ = Positively the same or homologous pattern; + = Similar or probably homologous pattern; ? = Description is hard to interpret; / = This pattern is described in an other behaviour pattern.

Appendix 7: Comparison Siamang and White-Cheeked Crested Gibbon Behaviour.

Abbreviations and symbols:

- This behaviour is not recorded quantitatively.
- 0 This behaviour has not been documented by any individual of the adequate age group.
- E This behaviour has been performed in a single case
- # About 1/3 of all individuals have performed this behaviour.
- ## Up to 2/3 of all individuals have performed this behaviour.
- ###: More than 2/3 of all individuals performed this behaviour
- Ssy: Siamang (*Symphalangus syndactylus*)
- Nle: White-cheeked crested gibbon (*Nomascus leucogenys*)

Behaviour	Adult Male		Adult Female		Subadult		Juvenile		Infant	
	Ssy n=16	Nle n=5	Ssy n=18	Nle n=5	Ssy n=10	Nle n=1	Ssy n=15	Nle n=0	Ssy n=9	Nle n=4
Take nipple in mouth	–	0	–	0	E	###	#	–	###	###
Bellycarrying	#	0	###	###	#	0	0	–	0	###
Bring in the infant	E	0	###	###	0	0	0	–	0	0
Reprimand the infant	–	###	–	###	–	###	–	–	–	0
Swing/hang	#	###	#	###	0	###	##	–	0	###
Make a tumble	E	#	E	0	E	###	##	–	#	###
Somersault	0	E	0	E	0	###	#	–	0	#
Jump	–	###	–	###	–	###	–	–	–	###
Climb	–	###	–	###	–	###	–	–	–	###
Brachiate	–	###	–	###	–	###	–	–	–	###
Free fall	–	–	–	–	–	–	–	–	–	–
Tumble around the rope	–	0	–	0	–	0	–	–	–	#
Cower	–	###	–	###	–	0	–	–	–	###
Swing on one arm	–	###	–	###	–	###	–	–	–	###
Walk bipedal	–	###	–	###	–	###	–	–	–	###
Sliding down rope/branch	–	–	–	–	–	–	–	–	–	–
Explorative grab at objects	–	E	–	#	–	0	–	–	###	#
Research object	–	#	–	0	–	0	–	–	–	#

Appendix 7. Continued

Behaviour	Adult Male		Adult Female		Subadult		Juvenile		Infant	
	Ssy n=16	Nle n=5	Ssy n=18	Nle n=5	Ssy n=10	Nle n=1	Ssy n=15	Nle n=0	Ssy n=9	Nle n=4
Bite in object	##	#	##	0	##	###	##	—	###	###
Get the object out of the water	—	#	—	#	—	0	—	—	—	#
Throw up and catch the object	—	0	—	E	—	###	—	—	—	##
Throw away/up the object	—	E	—	0	—	###	—	—	—	#
Object play rope/stick	—	E	—	0	—	0	—	—	—	##
Play with grass	—	E	—	0	—	###	—	—	—	###
To lay about the object	—	E	—	0	—	0	—	—	—	E
Inhibited bite	###	E	###	0	###	0	###	—	###	0
Grab at social partner	—	###	—	##	—	###	—	—	—	###
Grab at bird	—	##	—	E	—	0	—	—	—	0
Romp bite	###	###	###	###	###	###	###	—	##	###
Quick chase play	###	—	###	—	###	—	###	—	#	—
Quick chase aggressive	#	—	#	—	#	—	0	—	0	—
Push oneself between 2 animals	0	0	E	0	#	0	##	—	##	#
Observe	—	###	—	###	—	###	—	—	—	###
Reprimand the animal	—	0	—	#	—	0	—	—	—	0
Threat bite	—	#	—	0	—	0	—	—	—	0
Threaten	—	#	—	0	—	###	—	—	—	0
Wild impress	—	##	—	##	—	###	—	—	—	E
Pirouette	#	###	E	#	E	###	0	—	0	E
Grab grass	—	##	—	###	—	###	—	—	—	##
Catch food	—	##	—	###	—	###	—	—	—	0
Catch insect	—	###	—	###	—	###	—	—	—	###
Transport food	—	###	—	###	—	###	—	—	—	##

[illegible][illegible]

Appendix 8: Enclosure Variables of all Gibbon Groups

The size and surface of the enclosures of the 5 white-cheeked crested gibbon groups and the 12 siamang groups.

	Group	Enclosure form	Surface in m ²
White-cheeked crested gibbon (this study)	Apeldoorn	Gibbon island	250
		Inside enclosure	15
White-cheeked crested gibbon (Hold, 1998)	Amsterdam	Gibbon island	?
		Inside enclosure	?
	Beekse Bergen	Gibbon island	448
		Sleeping house	2
	Hannover 1	Gibbon island	?
		Sleeping house	?
	Hannover 2	Gibbon island	?
		Sleeping house	?
Siamang (Orgeldinger, 1999)	Branféré A	Gibbon island	356
		Sleeping box	?
	Branféré B	Gibbon island	422
		Sleeping box	?
	Budapest	Inside enclosure	30.7
	Dresden A	Inside enclosure	7.9
	Dresden B	Inside enclosure	7.9
	Duisburg a	Inside enclosure	23.6
	Duisburg b	Inside enclosure	23.6
	Frankfurt	Outside enclosure	21.7
		Inside enclosure	13
	Krefeld A	Inside enclosure	51.5
	Krefeld B	Outside enclosure	34.6
		Sleeping box	?
	München	Gibbon island	ca 35
		Inside enclosure	ca 55
	Studen-Biel	Outside enclosure	27
		Sleeping box	?