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Left: Bronze and silver monkey fitting. Late Eastern Zhou period, 4th-3rd century BC. Dimensions: length 18.2 cm. Source: Eskenazi (2000, pp. 38-41, no. 5). Courtesy of Eskenazi Ltd.– *Halterung aus Bronze und Silber, Östliche Zhou-Dynastie, 4.-3. Jahrhundert v. Chr.*

Right top: *A family of monkeys*. Attributed to Yi Yuanji (active mid-late 11th century, Northern Song dynasty, China). Ink and colour on silk. Dimensions: 50.5 x 82 cm. Source: Christie's (2000, p. 19, Lot 503). – *Gibbonfamilie. Yi Yuanji zugeschrieben (Mittleres bis spätes 11. Jahrhundert, Nördliche Song-Dynastie, China).*

Right bottom: *Gibbons and a bamboo grove*. Hasegawa Tohaku (1539-1610, Momoyama period, Japan). This is the left screen of a pair of six-panel screens; the right screen (not shown) depicts a bamboo grove, without gibbons. Ink and gold on paper. Dimensions of each screen: 154.0 x 361.8 cm. Collection of the Shôkoku-ji Temple, Japan. – *Gibbons und ein Bambushain. Hasegawa Tohaku (1539-1610, Momoyama-Periode, Japan).*

Instructions to Contributors

The Gibbon Journal publishes original papers in English or German on all aspects of gibbon natural history. It is distributed electronically and published annually by the Gibbon Conservation Alliance.

An English abstract is to be provided, preferably no longer than 250 words.

Figures and tables should be numbered and referred to by number in the text. Each figure and table should have an accompanying caption. Colour figures are welcome, but should be understandable if printed in black-and-white.

Citations in the text should include author name(s) and year in parentheses. Where there are three or more authors, only the first author's name is given in the text, followed by "*et al.*".

List cited references alphabetically at the end of the paper. Examples:

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Dem Manuskript soll eine englische Zusammenfassung von bis zu 250 Worten beiliegen.

Abbildungen und Tabellen sollten beide fortlaufend nummeriert sein und im Text genannt werden. Jede Abbildung und jede Tabelle sollte eine Legende haben. Farbabbildungen sind willkommen, sollten jedoch auch verständlich sein, wenn sie in schwarzweiss gedruckt werden.

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Theses: **Dissertationen:**

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Gibbon paintings in China, Japan, and Korea: Historical distribution, production rate and context

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Gibbons (the small apes of the family Hylobatidae) occupied in the past and still occupy today an important niche in Chinese – and for some time also in Japanese and Korean – cultures. Their importance can be assessed in the frequent depiction of gibbons in the figurative arts. This is the first study to quantify the production of gibbon paintings in various periods of these countries' history. A total of 818 gibbon paintings were surveyed. Results show that the earliest gibbon paintings are much older than suggested in some previous publications – both in China (pre-Song) and in Japan (pre-Momoyama). Moreover, because of the low sampling level of early Asian paintings, gibbon paintings as a genre in each of these countries may still have a much earlier origin than the date indicated by the earliest paintings found during this study. The genre originated in China and later spread to the neighbouring countries Japan and Korea, although artists had limited knowledge about the apes they painted because gibbons never naturally occurred in these countries. Chinese paintings depicted gibbons in a large number of functions and contexts, for instance as symbols of Daoist and Buddhist origin. In Japan, however, the genre was introduced by Zen (=Chan) monks, and the large majority of Japanese gibbon paintings depict the old Buddhist theme "Gibbons grasping for the reflection of the moon in the water". Stylistically, however, Chinese and Japanese gibbon paintings quickly drifted apart. The theme "Gibbons grasping for the reflection of the moon in the water" is not depicted in Korean paintings, but the small sample of Korean gibbon paintings found during this study precludes generalizations. The production rate of gibbon paintings/time in China underwent marked, previously undocumented fluctuations. During the period from 1525 to 1900, gibbon paintings were continuously, but not frequently, being produced in China. To judge by the number of preserved gibbon paintings from that time, the genre was apparently more popular in Japan than in China. The most dramatic increase in the production rate of gibbon paintings occurred in China during the 20th century. Whereas gibbon paintings as a genre had almost completely been abandoned in Japan during that time, China experienced a previously undocumented and apparently unprecedented increase both in the number of painters that produced gibbon paintings, as well as in the high number of gibbon paintings that were produced by some specialists among these painters. Possible reasons for these fluctuations are discussed. Finally, this study documents changes in style and context of gibbon paintings that occurred in various historical periods and discusses their possible causes.

Introduction

Gibbons are apes and thus are more closely related to humans than to monkeys (Geissmann, 2003; Groves, 2001). Although roughly 70% of all ape species are gibbons or small apes (family Hylobatidae), gibbons are, in most parts of the world, much less popular than their larger-bodied relatives, i.e. chimpanzees, gorillas and orang-utans. Yet, gibbons appear to have been the first apes to have had close relations with humans, and certainly have been the first to be made the object of literary and artistic compositions. Not only was the gibbon rich in symbolic meanings (like virtually every other subject traditionally favoured by Chinese painters and poets), but it also occupied a special niche in Chinese culture since more than 2,000 years, becoming "a symbol of the unworldly ideals of the poet and the philosopher, and of the mysterious link between man and nature", as Van Gulik observed in the preface of his seminal monograph on "The Gibbon in China" (Van Gulik, 1967).

Already during the Zhou dynasty (1027-221 BC), the gibbon emerged as a distinct presence when the Chinese singled out the gibbon as "the aristocrat among apes and monkeys" (Van Gulik, 1967, Preface). Daoists sought longevity and immortality by various disciplines, among the most important of which were breathing exercises, aimed at absorbing the largest amount of *qi* (a mystic fluidum sustaining the universe by its circulation) and making it circulate throughout the body. Excessively long limbs such as the gibbon's arms (or the crane's legs and neck) were thought to be conductive to this discipline. As a result, the gibbon was considered an "expert" in inhaling the *qi*, "thereby acquiring occult powers, including the ability to assume human shape, and to prolong their life to several hundred years" (Van Gulik, p. 38). In addition, gibbons (and cranes) are famous for their melodious calls and their graceful movements. Like the crane, gibbons were kept as pets by the literati (Silbergeld, 1987). In the Zhou dynasty gibbons still roamed over the virgin forests of central China.

From the Han dynasty (206 BC-AD 220) onward, references to gibbons in all literary forms are plentiful. The gibbon was characterized as more aloof and mystical in its solitary lifestyle, whereas the macaque was identified as being fickle, vulgar, and known to create a nuisance (Harper, 2001). The difference was even more accentuated in later periods. Liu Zongyuan's (= Liu Tsung-yüan, 773-819) "*Zeng wangsun wen*" ("Essay on the hateful monkey breed") portrays the macaque as the "bad monkey" in contrast to the gibbon as the "good monkey" (cited in, and translated by, Van Gulik, 1967, p. 58). During the Han, the gibbons had to abandon many parts of their natural range as large areas of land were brought under cultivation and many roads, bridges and canals were built. The gibbons still occurred in the mountain ranges along the border of Sichuan and Hubei where the Yangtze river flows east through a series of gorges. Their haunting calls in the gorges became the traditional symbol of melancholy of travellers far from home. As asserted by Van Gulik (1967), nearly every poet who wrote from the third to the seventh century referred to the graceful movements and the mournful calls of the gibbon, and references in Tang (AD 618-907) literature are even more numerous.

From the Song dynasty (AD 960-1279) onward, pictorial records of gibbons become available, and Chinese painters have pictured gibbons "in all shapes and attitudes" (Van Gulik, 1967). Yi Yuanji (a Hunan master active in the 1060s) may have been the first painter to specialise in painting gibbons, but he was certainly the first to achieve fame for his depictions of gibbons (Barnhart *et al.*, 1997). According to a eleventh-century biography by Guo Rexu (cited in Van Gulik, 1967, p. 79), Yi Yuanji "used to roam all over south Hubei and north Hunan, going more than a hundred miles into the Wanshou mountains; just to observe gibbons, deer and such like animals…". One of the most celebrated Chinese gibbon paintings and one of the most famous Zen paintings of all time in Japan is "*Mother Gibbon and Child*" (Barnhart *et al.*, 1997; Graham, 1991; Lovell, 1981) by the thirteenth-century artist Muqi, a native of Sichuan and a Chan (Zen) monk (Fig. 1). The painting is a component of Muqi's masterpieces "*Crane, White Robed Guanyin and Gibbon*": three paintings that can be most confidently ascribed to this artist (Cahill, 1960). Although it is unknown when they were united to form a triptych, it is known that they were bought between 1392 und 1408 by Ashikaga Yoshimitsu (1358-1408) and that they are kept in the Daitoku-ji, the great Zen Buddhist temple in Kyoto since 1567 (Wey 1974, cited in Epprecht *et al.*, 2001, p. 128). In the triptych, the bodhisattva Guanyin (Japan: Kannon), the Goddess of Mercy, is flanked by a crane on the left, and by a gibbon mother embracing her infant on the right. These paintings became the source for long traditions of gibbon paintings (with or without cranes and Guanyin) in Japan (Klein and Wheelwright, 1984b; Epprecht *et al.*, 2001).

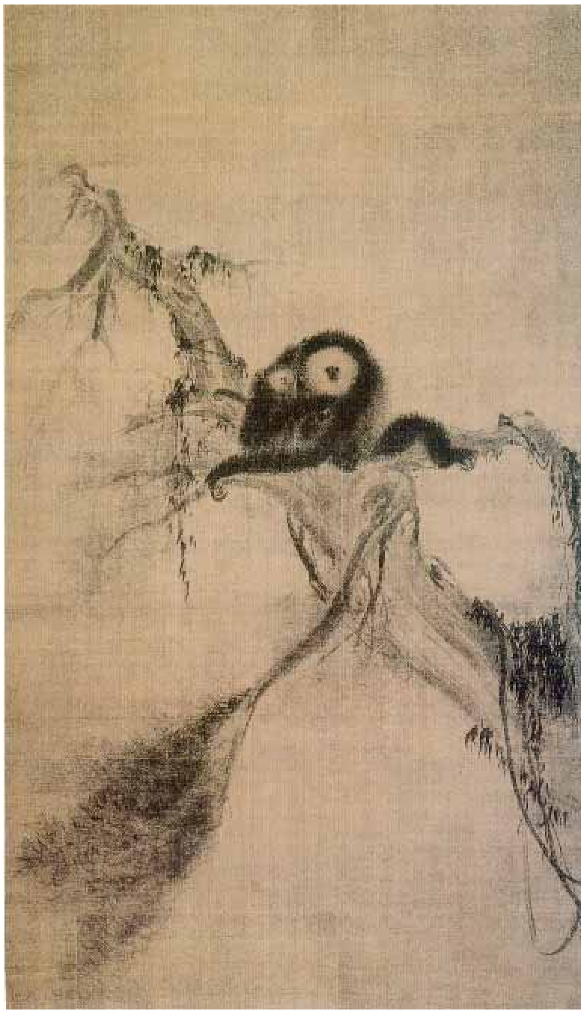

Fig. 1. *A gibbon with her baby on a pine branch*; right portion of the hanging scroll triptych *Crane, White Robed Guanyin, and Gibbon*. Muqi (c.1210- after 1269, Southern Song dynasty, China). Hanging scroll. Ink on silk. Dimensions: 173.9 x 99.4 cm. Daitoku-ji temple, Kyoto, Japan. Scan Number 0056671, courtesy of The John C. and Susan L. Huntington Archive, Ohio State University, College of the Arts. – *Gibbonmutter mit Kind auf einer Kiefer. Rechtes Bild eines Triptychons von Muqi (c.1210- nach 1269, Südliche Song-Dynastie, China).*

The gibbons' role in Chinese art and literature was so important, that the genre also spread to Japan and Korea, although neither country ever belonged to the gibbons' habitat. The history of gibbon paintings has only rarely been studied. The role of gibbons in Chinese (and Japanese) culture has been examined in considerable detail by Van Gulik (1967, pp. 97-99) and, to this day, every serious re-examination of this topic builds up on Van Gulik's monograph. The role of gibbons in Korean history was briefly summarised by Chon Chin-gi (2003). Tsumori (1997) surveyed Japanese paintings that depicted the popular subject known as "A monkey reaching for the moon". Although many gibbon paintings were doubtlessly included in the artworks he surveyed, the author did not distinguish between gibbons and monkeys.

Unfortunately, Van Gulik's "survey ends with the beginning of the Qing dynasty, in AD 1644; "for after that date the gibbon became so rare in China that what is written about him is largely repetitious" (Van Gulik, 1967, Preface). Van Gulik's fascination with depictions of gibbons in Chinese art was also limited to antique paintings. The most recent painting discussed in his monograph was painted by the Hsuan-te Emperor (= Hsüan-tsung, 1399-1435). He described the painting as "ably executed" but "not a great work of art". Because the gibbons in this painting were so life-like he wondered whether the emperor had used live models from the palace park. Yet, he found the brushwork devoid of force and the shoulders of one of the gibbons too broad and anatomically incorrect. He ended his evaluation of this particular painting as follows: "As it is, this picture compares favourably to most paintings of gibbons done in the later half of the Ming, and during the subsequent Ch'ing [Qing] dynasty that ruled China till the Revolution in 1912" (Van Gulik, 1967, p. 96). This single sentence is also the only reference to Chinese gibbon paintings that were created after the reign of Hsuan-te. There is no reference to gibbon paintings that were created after 1912. To this day, there appears to be no study that tried to examine more recent gibbon paintings. Furthermore, no attempt has apparently been made to examine the temporal distribution and changes in the production rate of gibbon paintings on a quantitative basis. Such changes could point to changes in the cultural role and importance of gibbons and could also be helpful in establishing a chronology of a hitherto unexamined but crucial subject.

The goal of this study is to fill out these gaps. Quantitative data collected during this study document that the production of Chinese gibbon paintings continued into modern times. Moreover, the genre actually appeared to experience its greatest popularity during the 20th century, whereas the production of gibbon paintings in Japan (and possibly Korea) was practically abandoned during the same period.

Methods

For the quantitative analysis, only paintings, drawings or woodblock prints (including art on fans and album leaves) were evaluated quantitatively. Sculptured gibbons (e.g. jewellery, belt buckles, carved *netsuke* (toggles)), gibbons in reliefs (e.g. on figure bricks, tea kettles, *inro* (lacquerware medicine boxes), *tsuba* (metal sword guards)), and gibbon designs on porcelain were also surveyed but not included in the quantitative analysis. Information on gibbon paintings was collected from the pertinent literature, from internet sources, and by directly contacting the curators of museum collections of Asian art and auction houses.

Only paintings that could be dated at least approximately were included in this study. If the exact year of creation was unknown (as was the case for the majority of the paintings), I estimated it by calculating an average of the earliest and latest date of creation, for instance using the dates of birth and death of the artist, or the earliest and the last known dates of an artist's known artistic career.

Gibbons are usually identified as apes "*yuan*" [猿] in Chinese and Japanese language, as compared to monkeys or "*hou*" [猴]. Gibbons are gracile, long-limbed and tail-less apes. Wild gibbons live and travel in the tree crowns. They exhibit an acrobatic arm-swinging type of locomotion when moving below tree-branches (brachiation) and walk on two legs (bipedal locomotion) when moving upon branches or on the ground (the latter being rarely seen in wild gibbons).

Not all gibbon paintings correctly depict gibbon anatomy, fur coloration and behaviour. This may have several causes. While some artists (for instance many painters of the "flowers and birds" genre during the Chinese Song dynasty) apparently strived to maximise naturalism (Cahill, 1960, p. 73f; Hesemann, 2006, p. 144, 158), form-likeness was absolutely not an important quality of a painting for many other artists, who rather tried to capture the 'spirit' or 'essence' of an object (Cahill, 1960, p. 89f; Hesemann, 2006, p. 144). Furthermore, depending on the artist's familiarity with gibbons and maybe also the artist's qualities, some of the painted animals resemble macaques more than gibbons, whereas other painted gibbons exhibit characteristics not seen in any living animal species.

In this study, gibbon paintings that clearly depicted macaques were excluded even if the painting's title identified the animal as an ape ("*yuan*"). Painted primates that exhibited at least some attributes typical of gibbons were included.

Dimensions of paintings in the figure legends indicate first height, then width.

Survey Results

China

Figure 2 shows the temporal distribution of the 636 Chinese gibbon paintings found during this survey versus time.

The rarity of gibbon paintings before 1200 suggests poor preservation of painted art from these times. Much earlier paintings probably existed but were lost. This view is supported by the observation that gibbons were featured in Chinese art well before the 9th century. Some of them are briefly presented below.

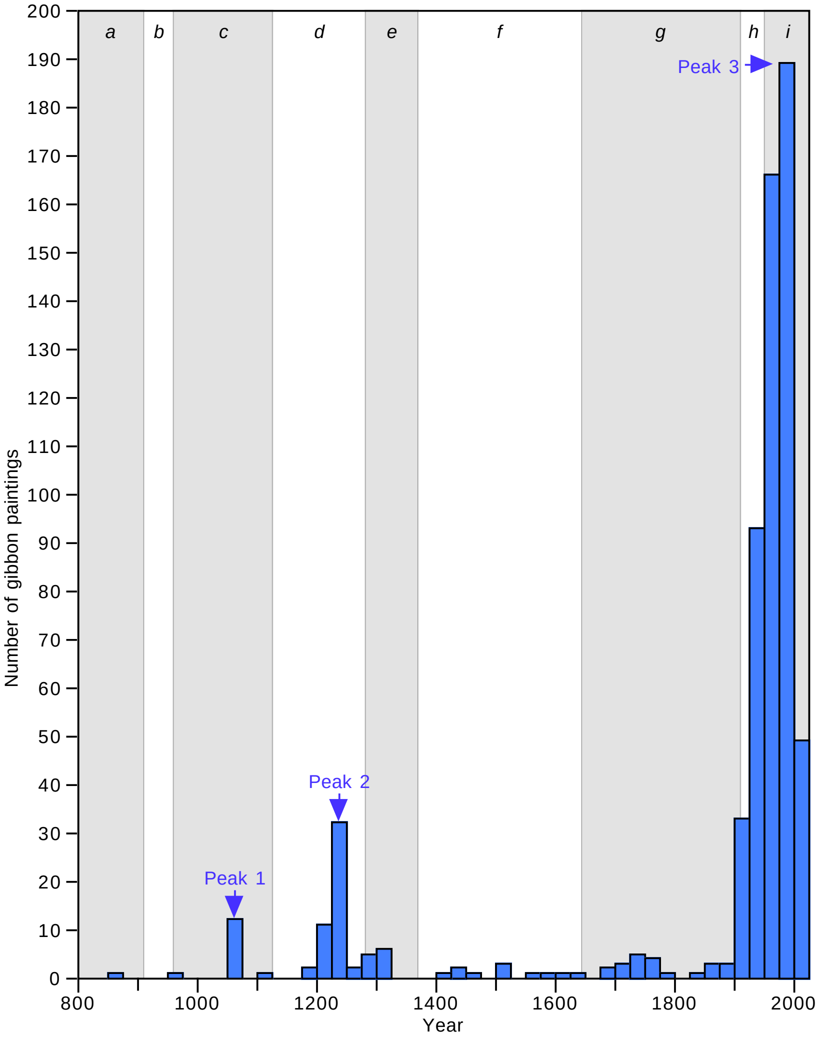

Fig. 2. Distribution of Chinese gibbon paintings versus time. Data: all known paintings until April 2008 ($n = 636$ paintings). Each blue bar represents the known gibbon paintings of a time period of 25 years. Alternating grey and white bars in the background represent the following periods and dynasties in Chinese chronology: (*a*) Tang: 618-907; (*b*) Five dynasties: 907-960; (*c*) Northern Song: 960-1126; (*d*) Southern Song: 1127-1279; (*e*) Yuan: 1279-1368; (*f*) Ming dynasty: 1368-1644; (*g*) Qing dynasty: 1644-1911; (*h*) Republic of China: 1911-1949; (*i*) The People's Republic of China: 1949-present. – *Geschichtliche Verbreitung von Gibbon-Gemälden in China (n = 636 Bilder). Jeder blaue Balken entspricht einem Zeitraum von 25 Jahren.*

Most of these early gibbon-shaped objects recorded during this study show a gibbon with its left arm stretched out forward and the other arm pointing in a different direction below the animal's body or behind it (e.g. Barrère, 2007; Museum of Fine Arts, Boston, 2007; Eskenazi, 1996, pp. 22-23; Liu, 1987, plate 299; Wang Tao, 2000, pp. 10-11; Zhongguo, 1980, vol. 2, plate 41, fig. 1). Gibbon-shaped objects of this type are known from the late Eastern Zhou period (4th-3rd century BC) and the Han dynasty (206 BC-AD 220). Two examples are shown in Figs. 3 and 4. Both wooden and metal versions of these gibbon objects exist. Several of them appear "to be wearing a trailing sash" (Eskenazi, 1996, p. 22) that looks as if the animal had a short tail (Fig. 3). The gibbons' hook-shaped hands were apparently designed to hold, or attach to, another object. Various functions have been proposed for these objects, including a garment-hook, a belt-hook or a belt-buckle, a ceiling fitting, or a piece of jewellery.

Fig. 3. Gilt and silvered bronze and turquoise garment-hook (*daigou*). Eastern Zhou dynasty, 4th-3rd century BC. Dimensions: length 13.5 cm. Source: Eskenazi (1996, pp. 22-23, no. 7). Courtesy of Eskenazi Ltd. – *Gewandhaken aus Bronze, vergoldet, versilbert und mit Türkis-Einlagen. Östliche Zhou-Dynastie, 4.-3. Jahrhundert v. Chr.*

Fig. 4. Bronze gibbon belt buckle. Han dynasty (206 BC - AD 220), Yunnan province. Dimensions: 10.3 x 0.33 x 0.17 cm. Unknown location. – *Gürtelschnalle aus Bronze. Han-Dynastie, 206 v. Chr. – 220 n. Chr.*

A different type of gibbon-shaped object is shown in Fig. 5. This bronze fitting, possibly one of a pair from which a hanging lamp was suspended, is cast as a gibbon with upstretched arms, inlaid all over in silver (Eskenazi, 2000, pp. 38). A gilded bronze gibbon of almost identical shape and size as the object described above dates from the Tang Dynasty (AD 618-907) (china-artweb.com, 2008).

A relief brick found in Xin'nongxiang (Xindu, Province Sichuan) and dating from the Eastern Han dynasty (AD 25-220) depicts an erotic scene observed by two gibbons hanging from a tree branch (Göpper, 1996, p. 412). This brick is reproduced in Fig. 6. According to Chen Lie (1996, pp. 411-413), the scene represents a springtime fertility rite that can be traced back to pre-Qing times (i.e. before 221 BC) and that is known as "worship of the Gaomei divinity". The whole scene, including the gibbons and

Fig. 5. Bronze and silver monkey fitting. Late Eastern Zhou period, 4th-3rd century BC. Dimensions: length 18.2 cm. Source: Eskenazi (2000, pp. 38-41, no. 5). Courtesy of Eskenazi Ltd.– *Halterung aus Bronze und Silber, Östliche Zhou-Dynastie, 4.-3. Jahrhundert v. Chr.*

Fig. 6. Figure brick depicting an erotic scene (*sangletu*) from a tile grave of the Eastern Han period (AD 25-220) from Xinnongxiang, Xindu county, Sichuan province. Ceramic, traces of reddish and black painting. Excavated in 1979. Dimensions: 29 x 50 cm. Collection of Xindu County Bureau of Cultural Antiquities. Source: Göpper (1996, p. 412, fig. 106:1). – *Reliefziegel mit erotischer Szene aus einem Ziegelgrab der Östlichen Han-Periode (25-220 n. Chr.) von Xinnongxiang im Kreis Xindu der Provinz Sichuan.*

the birds in the tree, may symbolize the "harmonious coexistence of humans and nature that re-awakens to a new strength in spring" (Chen Lie, 1996, p. 411).

The identities of a black primate on a tomb mural from the late second century AD (Eastern Han period) and of a grey-furred primate painted on a pre-Tang vase (i.e. dating before AD 618) are less clear (Greiff and Yin, 2002, p. 23 and fig. 36; Visser, 1926, plates I and II). These animals might represent gibbons, because they are both walking bipedally on long, slender hindlegs, but they might also be macaques, as their faces are red and they have short tails.

In the following part, I will present findings concerning paintings of gibbons. Some examples are shown in Figs. 7-28.

The earliest gibbon painting found during this survey was made by Guanxiu (832-912) (Fig. 7). It shows an arhat who is offered peaches by a gibbon. Arhats (or lohans) were disciples of the historical Buddha, which firmly establishes this painting in a Buddhistic context.

The second-oldest gibbon painting (not shown here) is known as "*Monkeys and horses*" (Palace Museum Collection, Taipei, Taiwan). It was originally attributed to Han Kan (8th ct.) but is now believed to be of more recent origin (10th ct.) (Cahill, 1960, p. 71).

A first peak in the number of gibbon paintings appears to have occurred during the Northern Song dynasty in the time slot of 1050-1075 (Fig. 2). All twelve paintings of this peak were made by, or attributed to, Yi Yuanji. As this artist's main activity period occurred in 1064-1067, all these paintings are assigned to the time slot of 1050-1075 in Fig. 2. By judging from the highly diverse styles of these paintings, however, it is unlikely that they were all made by the same artist. Some paintings attributed to Yi Yuanji are shown in Figs. 8-10.

Fig. 7. *Sixteen Arhats (Lohans) on sixteen scrolls* (one of sixteen hanging scrolls). Guanxiu (832-912, Five dynasties, China). Colour on silk. Dimensions: 128.9 x 65.8 cm. Kōdai-ji temple, Kyoto, Japan. – *Einer von "Sechzehn Arhats (Lohans) auf sechzehn Bilderrollen". Guanxiu (832-912 n. Chr., Fünf Dynastien, China)*.

Fig. 8. *Group of gibbons* (section). Attributed to Yi Yuanji (active mid-late 11th century, Northern Song dynasty, China). Handscroll. Dimensions: 32.5 x 120 cm. Osaka Municipal Museum of Art. – *Gruppe von Gibbons (Ausschnitt). Yi Yuanji zugeschrieben (Mittleres bis spätes 11. Jahrhundert, Nördliche Song-Dynastie, China)*.

Fig. 9. *A family of monkeys*. Attributed to Yi Yuanji (active mid-late 11th century, Northern Song dynasty, China). Ink and colour on silk. Dimensions: 50.5 x 82 cm. Source: Christie's (2000, p. 19, Lot 503). – *Gibbonfamilie. Yi Yuanji zugeschrieben (Mittleres bis spätes 11. Jahrhundert, Nördliche Song-Dynastie, China)*.

Fig. 10. *Gibbons and deer*. Attributed to Yi Yuanji (active mid-late 11th century, Northern Song dynasty, China). Round fan painting mounted as album leaf. Ink and colour on silk. Dimensions: 25 x 26.4 cm. National Palace Museum, Taipei, Taiwan, No. VA15f. – *Gibbons und Hirsche. Yi Yuanji zugeschrieben (Mittleres bis spätes 11. Jahrhundert, Nördliche Song-Dynastie, China)*.

A second peak in the number of gibbon paintings appears to have occurred in the time period from 1200 to 1325, starting halfway through the Southern Song dynasty and continuing well into the Yuan dynasty. Various artists contributed to these 56 gibbon paintings, but 32 of the paintings (57%) are attributed to Muqi (c.1210-1325). Some of his paintings are shown in Figs. 1, 11, and 12. It is obvious that gibbons were more often depicted in Chinese paintings from this period than in the periods immediately before and after it.

Fig. 11. (a) *Gibbon*. Attributed to Muqi (c.1210- after 1269, Southern Song dynasty, China). Hanging scroll. Ink on silk. Dimensions: 80.6 x 38.5 cm. University of California, Berkeley Art Museum, no. CY.12. On extended loan from the Sarah Cahill Collection. – *Gibbon. Muqi zugeschrieben (c.1210- nach 1269, Südliche Song-Dynastie, China)*.

Fig. 12. *Mother Gibbon and Child*. Attributed to Muqi (c.1210- after 1269, Southern Song dynasty, China). Hanging scroll. Ink on silk. Dimensions: 75.3 x 47 cm. University of California, Berkeley Art Museum, no. CY.13. On extended loan from the Sarah Cahill Collection. – *Gibbonmutter mit Kind. Muqi zugeschrieben (c.1210- nach 1269, Südliche Song-Dynastie, China)*.

Fig. 13. *Clearing out a mountain forest* (*Battling demons in a forest*), detail. Unknown artist (Ming dynasty, 15th-16th century, China). Handscroll. Ink on paper. Dimensions of the painting: 46.7 x 807.4 cm. Freer Gallery of Art, Smithsonian Institution, Washington, D.C., F1917.184. Gift of Charles Lang Freer. – *Einen Bergwald ausräumen (Kampf gegen Dämonen in einem Wald). Ausschnitt aus einer horizontalen Bildrolle. Unbekannter Künstler, Ming-Dynastie, 15.-16. Jahrhundert)*.

Following the second peak described above, gibbons remained a constant, albeit infrequent topic of Chinese paintings from about 1325 to 1900. Some examples are shown in Figs. 13-18.

Wild gibbons and their habitat were disappearing fast and by the 20th century, gibbons had become extinct over most of their previously large distribution area in China. Unlike some paintings from the preceding Song dynasty, gibbons in later paintings often exhibit inaccurate anatomical features, body proportions, or positional behaviours, suggesting that the artists may have been less familiar with real gibbons. For instance, painted gibbons may exhibit a short tail (like the group of sitting gibbons in section two of Fig. 17) or a fox-like pointed snout (Fig. 18), or they may hang from a branch by their elbows or axillas, although none of these features occur in natural gibbons.

Fig. 14. *Two gibbons in a tree*. Unknown artist (Ming dynasty, 15th century, China), in the style of Yi Yuanji (active mid-late 11th century). Hanging scroll (mounted on panel). Ink and colour on silk. Dimensions: 190.7 x 100.2 cm. Freer Gallery of Art, Smithsonian Institution, Washington, D.C., F1911.272. Gift of Charles Lang Freer. – *Zwei Gibbons auf einem Baum. Unbekannter Künstler im Stil von Yi Yuanji (Ming-Dynastie, 15. Jahrhundert, China)*.

Fig. 15. *Leashed gibbon stealing fruit*. Unknown artist (Ming dynasty, probably early 17th century). Previously attributed to Yi Yuanji (active mid-late 11th century, China). Hanging scroll (mounted on panel). Ink and colour on silk. Dimensions: 96 x 54.2 cm. Freer Gallery of Art, Smithsonian Institution, Washington, D.C., F1916.47. Gift of Charles Lang Freer. – *Angeleinter Gibbon beim Früchtestehlen. Unbekannter Künstler (Ming-Dynastie, vermutlich frühes 17. Jahrhundert, China)*.

Fig. 16. *Man and servant searching for plum blossoms; gibbon in a tree*. Attributed to Wang Hui (Qing dynasty, 17th to early 18th century, China). Hanging scroll. Ink and light colour on silk. Dimensions: 92.7 x 37.5 cm. University of California, Berkeley Art Museum, no. 1990.13. Gift of James Cahill. A small gibbon hanging from a branch and observing the two men can be seen near the left margin (upper third) of the painting. – *Mann und Diener auf der Suche nach Pfirsichblüten. Wang Hui zugeschrieben (Qing-Dynastie, 17. bis frühes 18. Jahrhundert, China). Ein kleiner Gibbon hängt an einem Ast und schaut zu (linker Bildrand, oberes Bilddrittel)*.

Fig. 17. *Landscape with gibbons and cranes*. Unknown artist (Qing dynasty, 18th century, China). Previously attributed to Qiu Ying (c.1494-1557). Handscroll. Ink and colour on silk. Dimensions of the painting: 27.7 x 271.1 cm. Freer Gallery of Art, Smithsonian Institution, Washington, D.C., F1904.396. Gift of Charles Lang Freer. The figure shows two of three scroll sections. In the first section (not shown), there are two cranes flying in the sky above one black and one white gibbon. – *Landschaft mit Gibbons und Kranichen. Unbekannter Künstler (Qing-Dynastie, 18. Jahrhundert, China). Diese Abbildung zeigt zwei von drei Abschnitten einer horizontalen Bildrolle. Der erste, hier nicht abgebildete Abschnitt zeigt zwei Kraniche, die einen schwarzen und einen weissen Gibbon überfliegen*.

Fig. 18. *Gibbon on rock*. Wang Englong (approx c.1844, Qing dynasty, China). Fan painting converted to album leaf. Ink and colours on silk. © The Trustees of the British Museum, London, no. 1973,0917,0.59.39. Used by permission. – *Gibbon auf einem Felsen. Wang Englong (c.1844, Qing-Dynastie, China)*.

After 1900, the number of gibbon paintings/time rises abruptly and steeply until 1975, as shown in Fig. 2. A total of 189 gibbon paintings were found from the single time slot of 1975 to 1999, i.e. during the third peak. All in all, 481 gibbon paintings were created during the 20th century, which is 4.5 times the number of the known gibbon paintings dating from all previous centuries. The most prolific gibbon painter of the 20th century was Tian Shiguang (1916-1999), who produced 65 gibbon paintings (i.e. 15.3%) of the gibbon paintings of the 20th century. Liu Wanming (1968-present) is even more specialized in gibbon paintings (119 paintings were found during this survey), but only a part of his oeuvre was produced during the 20th century. To this day, he still creates gibbon paintings.

The last bar (2000-2025) in the histogram of Fig. 2 is shorter because it only includes data from the time period from 2000 to April 2008, which implies that the production rate of gibbon paintings is not necessarily on its downswing after its peak in the second half of the 1990s.

Some exemplary gibbon paintings from the 19th and 20th century are shown in Figs. 19-28.

Fig. 19. *Gibbon and peaches*. Attributed to Gao Qifeng (1888-1933, China). Hanging scroll, ink and colours on paper. Dimensions of the painting: 128.5 x 66 cm. Private collection, Switzerland. – *Gibbon und Pfirsiche. Gao Qifeng zugeschrieben (1888-1933, China)*.

Fig. 20. *Climbing gibbons*. Pu Xinyu (= Pu Ru, 1896-1963, China). Hanging scroll, ink and colours on paper. Dimensions of the painting: 94 x 33 cm. Unknown location. Source: www.jingp.com. – *Kletternde Gibbons. Pu Xinyu (= Pu Ru, 1896-1963, China)*.

Fig. 21. *Sleeping gibbon*. Zhang Daqian (1899-1983, painted c.1934, China), signed as Liang Kai (active early 13th century). Hanging scroll. Ink on paper. Dimensions: 163.7 x 67.1 cm. Arthur M. Sackler Gallery, Smithsonian Institution, Washington, D.C., Jr, S2002.6. Gift of Patricia Falk, from the collection of Mr. and Mrs. Myron S. Falk. – *Schlafender Gibbon. Zhang Daqian (1899-1983, gemalt c.1934, China), signiert als Liang Kai (Maler des frühen 13. Jahrhunderts)*.

Fig. 22. *Gibbons fetching the moon from the water*. Chen Wenxi (1906-1992, painted early 1970s, Singapore). Chinese ink and colour on paper. Dimensions of painting: 181.5 x 97 cm. National University of Singapore Museum Collection (ref. S0001-0105-001-0). – *Gibbons greifen nach dem Spiegelbild des Mondes im Wasser. Chen Wenxi (1906-1992, gemalt in den frühen 1970er Jahren, Singapore)*.

Qi Baishi (1863-1957) may have been one of the first artists to draw gibbons in what looks like a "cartoony" style, with strongly exaggerated facial expressions. Some artists like Xie Zhiguang (1900-1976) clearly patterned their gibbon paintings after his, while others developed their own "cartoony" styles when depicting gibbons, for instance Zhang Qiyi (1915-1968) or Liu Wanming (1968-present) (Figs. 24, 28). Some artists like Zhang Daqian (1899-1983), Chen Wenxi (= Chen Wen Hsi, 1906-1992), or Fang Chuxiong (1950-present) developed more naturalistic gibbon depictions (Figs. 22-23, 27) which were at least in some, and probably most, cases facilitated by the artists' access to pet gibbons or zoo gibbons.

In Chinese paintings, gibbons are often depicted solitary, or in groups of two, three or five individuals. Paintings depicting large herds of dozens of gibbons also occur (Figs. 8, 17, 22), but are uncommon. Recurrent topics include gibbons accompanying an arhat, or gibbons collecting, carrying or offering peaches (Figs. 7, 19). A repeated theme in Song paintings is gibbons raiding a nest of egrets or herons and stealing young birds. The Buddhist theme "Gibbons reaching for the reflection of the moon" occurs as early as about AD 1200, but the theme remains uncommon in China and most paintings of this type are found in the 13th century.

Painted gibbons usually exhibit a black or dark coat with a white face-ring. White or light gibbons already occurred in the earliest gibbon paintings but remained relatively rare (Figs. 8, 10). Only occasionally, gibbons in various hues of brown, ochre, orange, yellow, or grey also occurred in Chinese paintings (Figs. 9, 17). White gibbons became much more common, however, in paintings of the 20th century (Figs. 20, 24), starting about in the 1930s with painters like Zhang Shanzi (1882-1940). Some artists like Tian Shiguang (1916-1999) actually specialized in painting white gibbons (Fig. 26). Whereas traditional Chinese gibbon paintings often are monochrome or exhibit relatively few colours, the use of bright colours become more common in gibbon paintings in the 20th century. A theme that becomes particularly popular among many gibbon painters of the 20th century, are gibbons in "autumnal trees" or trees with red leaves (Figs. 20, 24, 26, 27). The earliest dated paintings of this type stem from 1934 (Pu Xin-yu, 1896-1963) and 1935 (Zhang Shanzi, 1882-1940) (Fig. 20). Such paintings reflect the increased dominance of red colours in Chinese paintings during the 20th century.

Pre-Song objects with gibbon design or decoration were presented at the beginning of this section. Objects with gibbon designs continued to be produced later on, especially during the Qing dynasty (1644-1911), until today. Although such objects were not quantified during this study, they appeared to be much less common than similar objects in Japan. They included snuff boxes, cups, vases, tobacco jars, and porcelain figures.

Fig. 23. *Gibbons*. Chen Wenxi (1906-1992, painted c.1988, Singapore). Chinese ink and colour on paper. Dimensions of painting: 66.5 x 66.5 cm. Collection of the Art Galleries at Nanyang Academy of Fine Arts, S/N 137 (ref. C-FB-D 032/0115). – *Gibbons. Chen Wenxi (1906-1992, gemalt c.1988, Singapur)*.

Fig. 24. *Red autumn leaves and a pair of gibbons*. Zhang Qiyi (1915-1968, China). Colour on paper. Dimensions: 65 x 43 cm. Unknown location. Image publication by courtesy of ARTkaoshi (www.artkaoshi.com). – *Rote Herbstblätter und ein Gibbonpaar. Zhang Qiyi (1915-1968, China)*.

Fig. 25. *Gibbon calling on oak tree*. Xie Zhiliu (1910-1997, China, painted 1947). Hanging scroll, ink and colour on silk. Dimensions: 105 x 51 cm. Unknown location. Source: Christie's (2007, p. 216, Lot 1207). – *Rufender Gibbon auf Eichenbaum. Xie Zhiliu (1910-1997, China, gemalt 1947)*.

Fig. 26. *White gibbon with autumn leaves*. Tian Shiguang (1916-1999, China). Hanging scroll, ink and colour on paper. Dimensions: 132 x 64 cm. Unknown location. Source: www.zhuokearts.com. – *Weisser Gibbon mit Herbstblättern. Tian Shiguang (1916-1999, China)*.

Fig. 27. *Hearing the gibbons from an autumnal mountain*. Fang Chuxiong (1950-present, painted 1988, China). Ink and colour on paper. Dimensions: 68.5 x 136.5 cm. Unknown location. Source: http://artso.artron.net – *Gibbonrufe klingen vom Herbstwald. Fang Chuxiong (1950-heute, gemalt 1988, China)*.

Fig. 28. *Happiness*. Liu Wanming (1968-present, China). Ink and colour on paper. Dimensions: 69 x 69 cm. Unknown location. Source: www.zhuokearts.com. – *Glück. Liu Wanming (1968-heute, China)*.

Japan

Figure 29 shows the temporal distribution of the 172 Japanese gibbon paintings found during this survey versus time.

The earliest known gibbon painting is attributed to Kyōdō Kakuen (1244-1306) and bears an inscription by Jingtang Jueyuan (= Ching-t'ang Chüeh-yüan, 1244-1306), who came to Japan in 1279 (Toda Teisuke, 1973, p. 171, fig. 73). The second known painting is a scroll depicting the *Death of the historical Buddha* in the Langen collection (Germany). It was made by an unknown artist and is dated to the Kamakura period of the 14th century (Miyeka, 1998, pp. 18-19).

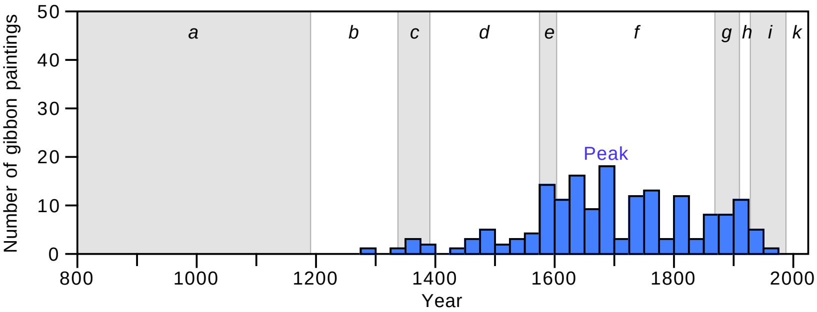

Fig. 29. Distribution of Japanese gibbon paintings versus time. Data: all known paintings until April 2008 ($n = 172$ paintings). Each blue bar represents the known gibbon paintings of a time period of 25 years. Alternating grey and white bars in the background represent the following periods in Japanese chronology: (*a*) Heian: 794-1192; (*b*) Kamakura: 1192-1334; (*c*) Nambokucho: 1334-1392; (*d*) Muromachi: 1392-1573; (*e*) Azuchi-Momoyama: 1573-1603; (*f*) Edo: 1603-1868; (*g*) Meiji: 1868-1912; (*h*) Taisho: 1912-1926; (*i*) Showa: 1926-1989; (*k*) Heisei: 1989-present. – *Geschichtliche Verbreitung von Gibbon-Gemälden in Japan (n = 172 Bilder). Jeder blaue Balken entspricht einem Zeitraum von 25 Jahren.*

From the 14th to the 16th century, the number of gibbon paintings is increasing relatively steadily in time (Fig. 29). The output reaches a peak during the 17th century and then diminishes more or less steadily until the end of the 20th century. No gibbon paintings produced after 1970 were found during this survey.

During about 700 years, gibbons enjoyed a continued presence in Japanese paintings, and no clear temporal subdivisions can be recognized from the frequency distribution shown in Fig. 29. It should be noticed, however, that the data set of Japanese gibbon paintings ($n = 172$) available for this study is more than three times smaller than that for China ($n = 636$). Likewise, the time period during which gibbon paintings were produced is much shorter for Japan than for China. Interestingly, a comparison between Figs. 2 and 29 reveals that consistently more gibbon paintings are available from Japan than from China during the time period from 1525 to 1900.

Several examples of the Japanese gibbon paintings are shown in Figs. 30-42. No single artist appears to have played a dominant role in the output of the Japanese gibbon paintings. The best represented artists in this data set are Hakuin Ekaku (1685-1768) and Hashimoto Kansetsu (1883-1945), who each contributed nine paintings (Figs. 39 and 42).

Like in China, gibbons painted by Japanese artists usually exhibit a black or dark coat with a white face-ring. Light gibbons occur in many paintings, but remain a minority. Most Japanese gibbon paintings are monochrome or exhibit few colours. The majority of the paintings depict the theme of the “Gibbon reaching for the moon” or “Gibbon reaching for the reflection of the moon in the water”. Paintings of gibbon chains – i.e. gibbons hanging down from trees attached to one another in chains to touch the reflection of the moon – are quite common (Fig. 38).

As a general trend in Japanese gibbon painting, gibbons were often depicted as cuddly hairballs with big, round, fluffy heads and very small faces (Fig. 31, 35). As another trend, artists like Tawaraya Sotatsu (1600-1640), Hakuin Ekaku (1685-1768) or Ogata Gekko (1900-1911) depicted gibbons with increasingly long arms (Fig. 41).

Fig. 30. *Gibbon*. Shugetsu (1440?-1529, Muromachi period, Japan). Hanging scroll. Ink on paper. Dimensions of the painting: 93.8 x 32.8 cm. Freer Gallery of Art, Smithsonian Institution,

Washington, D.C., F1996.29. Gift of Mary Keetch and Charles L. Vincent. – *Gibbon. Shugetsu (1440?-1529, Muromachi-Periode, Japan)*.

Fig. 31. *Monkeys and trees on a river bank*. Attributed to Sesson Shukei (1504-1589) or Sesson school (Momoyama period, 1573-1615, Japan). Pair of six-panel screens. Ink on paper. Dimensions of each screen: 176.5 x 371.1 cm. Freer Gallery of Art, Smithsonian Institution, Washington, D.C., F1903.218-.219. Gift of Charles Lang Freer. – *Affen und Bäume am Flussufer. Sesson Shukei zugeschrieben (1504-1589) oder Sesson-Schule (Momoyama-Periode, 1573-1615, Japan)*.

Fig. 32. *Gibbons and a bamboo grove*. Hasegawa Tohaku (1539-1610, Momoyama period, Japan). This is the left screen of a pair of six-panel screens; the right screen (not shown) depicts a bamboo grove, without gibbons. Ink and

gold on paper. Dimensions of each screen: 154.0 x 361.8 cm. Collection of the Shôkoku-ji Temple, Japan. – *Gibbons und ein Bambushain. Hasegawa Tohaku (1539-1610, Momoyama-Periode, Japan)*.

Fig. 33. *Monkey*. Unknown artist (around 1600, Momoyama period, Japan). Ink on paper. Dimensions: 98.1 x 42 cm. Museum of East Asian Art in Cologne, Germany, Inv. no. A 77,48. Gift of Kurt Brasch. – *Affe. Unbekannter Künstler (um 1600, Momoyama-Periode, Japan)*.

Fig. 34. *Mother gibbon reaching for the moon*. Unknown artist Hasegawa school (around 1600, Momoyama period, Japan). Ink on heavy paper. Dimensions of scroll: 119.4 x 51.4 cm. Private collection of the late Gordon Smith (Los Angeles, California). A forged Sesshu signature and stamp were added to deceive potential buyers. This painting may have been part of a sliding door or wall painting, judging by the unusually thick paper. – *Gibbonmutter versucht, den Mond zu fassen. Unbekannter Künstler, Hasegawa-Schule (um 1600, Momoyama-Periode, Japan)*.

Fig. 35. *Twelve gibbons reaching for the moon*. Unknown artist, Hasegawa school (around 1610, Edo period, Japan). Folding fan mounted on scroll. Opaque colours on gold leaf. Dimensions of scroll: 48.3 x 21.6 cm. Private collection of the late Gordon Smith (Los Angeles, California). – *Zwölf Gibbons versuchen, den Mond zu fassen. Unbekannter Künstler, Hasegawa-Schule (um 1610, Edo-Periode, Japan)*.

Fig. 36. *Kannon and gibbons*. Kano Naonobu (1607-1650) and Kano Tsunenobu (1636-1713, Edo period, Japan). The gibbon paintings form the two lateral elements of a triptych, with the central piece (not shown) depicting Kannon, the Buddhist Goddess of Mercy. Hanging scrolls, ink on paper. Dimensions of each scroll: 118.5 x 49.7 cm. The University Art Museum, Tokyo National University of Fine Arts and Music. Catalogue no. 1916-25577, classification no. 1916. – *Kannon und Gibbons. Kano Naonobu (1607-1650) und Kano Tsunenobu (1636-1713, Edo-Periode, Japan). Die beiden Gibbonbilder sind die Seitenbilder eines Triptychons. Die mittlere Bildrolle (hier nicht abgebildet), zeigt Kannon, die buddhistische Göttin der Gnade*.

Fig. 37. *Monkeys playing on oak branches*. Hasegawa School (1615-1868, Edo period, Japan). Pair of hanging scrolls, ink and colours on paper. Dimensions of each painting: 177.5 x 138.4 cm. Gift and Purchase from the Harry

G. C. Packard Collection Charitable Trust in honour of Dr. Shujiro Shimada; The Avery Brundage Collection, 1991.62.1 (right) and 1991.62.2 (left). © Asian Art Museum of San Francisco. Used by permission. Although the museum title of the two paintings refers to monkeys, the artist was obviously depicting gibbons. The paintings' large scale and evidence on each that a door-catch has been removed attest that they were once sliding doors (*fusuma*). – *Spielende Affen auf Eichenästen. Unbekannter Künstler, Hasegawa-Schule (1615-1868, Edo-Periode, Japan)*.

Fig. 38. *Gibbon chain*. Kano Minenobu (1662-1708, Edo period, Japan). Ink and light colours on silk. Dimensions of painting 99.1 x 31.1 cm. Private collection of the late Gordon Smith (Los Angeles, California). – *Gibbon-Kette. Kano Minenobu (1662-1708, Edo-Periode, Japan)*.

Fig. 39. *Long-armed Monkey*. Hakuin Ekaku (1685-1768, Japan). Hanging scroll, ink on paper. Dimensions: 117.3 x 57.4 cm. Eisei-Bunko Museum, Tokyo. – *Langarmiger Affe. Hakuin Ekaku (1685-1768, Japan)*.

Fig. 40. *Monkeys*. Made after Morikage Kusumi (c.1620-1690; print created c.1930s, Showa period, Japan). Signature: zen Hokusai I'itsu. Woodcut print from the Robert O. Muller Estate, colour on paper. Publisher Distributor: Shima Art Company. Dimensions: 17 x 39 cm. Image publication by courtesy of artelino Gmbh. – *Affen. Nach Morikage Kusumi (c.1620-1690; Holzschnitt hergestellt c.1930er Jahre, Showa-Periode, Japan)*.

As mentioned above, early Japanese depictions of gibbons were strongly influenced by Chinese paintings. Interestingly, an influence in the opposite direction did also occur to some extent during the 20th century, as gibbon paintings by the famous Japanese artist Hashimoto Kansetsu (1883-1945) (Fig. 42) inspired several Chinese artists such as Hu Zaobin (1897-1942), Wang Zhaoxiang (1910-1988), Zhao Yunyu (1916-2003).

Objects decorated with gibbon designs, although not quantitatively evaluated in this study, appear to be more common in Japan than in China or Korea. Especially during the Edo period (1603-1868) and the Meiji period (1868-1912), gibbons were depicted on a multitude of objects including writing utensil boxes (*suzuribako*), lacquerware medicine boxes (*inro*), cigarette boxes, perfume boxes, incense boxes, carved toggles (*netsuke*), paper knifes, jewellery, dishes, tea cups, tea kettles, metal sword guards (*tsuba*) and sword pommels (*fuchikashira*), handles of small blades (*kozuka*), and body armour. As in Japanese gibbon paintings, the most common theme of these gibbon designs is “Gibbon reaching for the moon”.

Fig. 41. *Monkey and the moon reflection*. Ogata Gekko (1859-1920, created c.1900, Meiji period, Japan). Woodcut print from the Robert O. Muller Estate, colour on paper. Publisher: Daikoku-ya (Tokyo, 1818-1923). Dimensions: 24.0 x 24.5 cm (*shikishiban* format). Image publication by courtesy of artelino Gmbh. – *Affe und die Spiegelung des Mondes. Ogata Gekko (1859-1920, Holzschnitt hergestellt c.1900, Meiji-Periode, Japan)*.

Fig. 42. *Black gibbons*. Hashimoto Kansetsu (1883-1945, painted 1933, Japan). Colour on silk. Dimensions: 139.9 x 158.0 cm. The University Art Museum, Tokyo National University of Fine Arts and Music. Catalogue number 1983-459, classification no. 960. – *Schwarze Gibbons. Hashimoto Kansetsu (1883-1945, gemalt 1933, Japan)*.

Korea

Only 14 gibbon paintings from Korea were found during this study. They are distributed across the time period from 1550 to 1950, as shown in Fig. 43.

The small sample size does not allow to recognize the presence of a pattern of occurrence in time (if any), but it may be mentioned that none of the Korean paintings falls outside the temporal distribution range of gibbon paintings in Japan (see Fig. 29). The artist’s name is known for only eight of these paintings, and only two of these artists produced more than one gibbon painting (Yun Duseo, *n* = 2, and Jang Seung-eop, *n* = 2).

Some examples of the Korean gibbon paintings are shown in Figs. 44-47.

Gibbons in Korean paintings exhibit a great variability in anatomy and fur colouration, often depicting features that do not naturally occur in gibbons, including gibbons that do not hang from a branch by their hands but by their axillas (Fig. 45), gibbons with unusually flat heads and long snouts (Fig. 46), or gibbons with short tails (Fig. 47).

Five of the paintings depict gibbons holding or gathering peaches (Daoist symbols of longevity). Only one painting can be placed in a Buddhist context as it combines the gibbon or gibbon-like animal with a Buddhist monk.

Objects with gibbon design include porcelain jars from the 17th and 18th centuries decorated with grapes and gibbons.

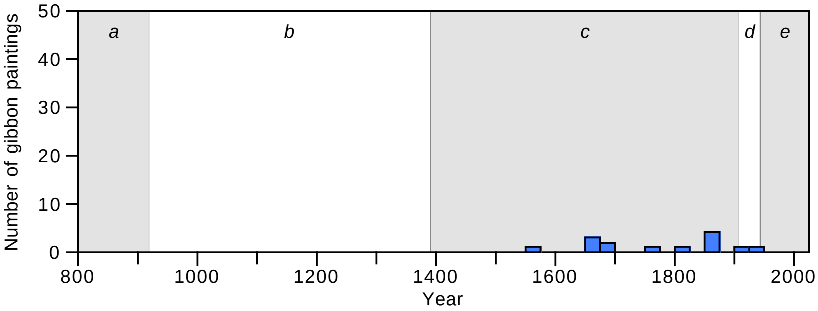

Fig. 43. Distribution of Korean gibbon paintings versus time. Data: all known paintings until April 2008 ($n = 14$ paintings). Each blue bar represents the known gibbon paintings of a time period of 25 years. Alternating grey and white bars in the background represent the following periods in Korean chronology: (*a*) Unified (or Great) Silla dynasty: 668-918; (*b*) Koryo dynasty: 918-1392; (*c*) Yi (or Choson) dynasty: 1392-1910; (*d*) Japanese colonial period: 1910-1945; (*e*) 1945-present. – *Geschichtliche Verbreitung von Gibbon-Gemälden in Korea (n = 14 Bilder). Jeder blaue Balken entspricht einem Zeitraum von 25 Jahren*.

Fig. 44 (left). *Gibbons and deer*. Attributed to Yun Om (1536-1581, Korea). Colour on silk. Dimensions: 178.5 x 109.7 cm. National Museum of Korea, Seoul. – *Gibbons und Hirsch. Yun Om zugeschrieben (1536-1581, Korea)*.

Fig. 45 (below). *Swinging gibbon*. Yun Duseo (= Kong-jae) (1668-1718, Korea). Dimensions of scroll: 22 x 19 cm. Ink on silk. Collection of The Honorable and Mrs. Joseph P. Carroll. Photo: Thierry Ollivier / Musée des arts asiatiques Guimet, Paris, 136_04K233. – *Hängender Gibbon. Yun Duseo (= Kong-jae) (1668-1718, Korea)*.

Fig. 46. *Two gibbons in a tree*. Kim Ikchu (Kyongam) (probably around late 18th /early 19th century, Korea). Dimensions: 26.6 x 19 cm. National Museum of Korea, Seoul. – *Zwei Gibbons auf einem Baum. Kim Ikchu (= Kyongam, vermutlich spätes 18./ frühes 19. Jahrhundert, Korea).*

Fig. 47. *Gibbon*. Lee Yongwoo (1904-1952, painted 1940, Korea.). Colour on paper. Dimensions: 54 x 57 cm. Leeum, Samsung Museum of Art, Seoul. – *Gibbon. Lee Yongwoo (1904-1952, gemalt 1940, Korea).*

Temporal distribution and individual output of gibbon artists

As demonstrated above (Figs. 2 and 29), several distinct peaks in the number of gibbon paintings can be distinguished in Chinese and Japanese art history. The occurrence of similar maxima in Korean gibbon paintings cannot be assessed because of the small size of the Korean sample.

In order to eliminate individual differences in productivity, Fig. 48 shows the temporal distribution of all Chinese and Japanese gibbon painters identified during this survey versus time. The resulting two histograms closely resemble the plots of paintings versus time (Figs. 2 and 29), demonstrating that the peaks in productivity are not only the result of the high output of few individual artists. Only the first peak is not visible in Fig. 48a, because it consisted solely of paintings attributed to one single painter (Yi Yuanji).

Figure 48b suggests that the temporal distribution of Japanese gibbon painters may exhibit a second peak during the first half of the 19th century. This was not obvious in the temporal distribution of Japanese gibbon paintings shown in Fig. 29.

In order to study the productivity of the various painters, I determined the number of gibbon paintings found for every Chinese and Japanese gibbon artist and plotted it versus the main activity period or mid-life time of each artist (Fig. 49). A total of 25 Chinese and 29 Japanese paintings were excluded from this part of the study, because their authorship was unknown. Whereas the Chinese paintings of unknown authorship are about evenly distributed across the whole production period of Chinese gibbon paintings, with a weakly defined peak in the 13th/14th centuries ($n = 6$ and 5, respectively), Japanese paintings of unknown authorship show a similar frequency distribution as the whole sample of Japanese paintings, with the majority of them (n = 10 paintings) clustered in the time period of the 17th century.

Figure 49a reveals that the first peak in the number of Chinese gibbon paintings consists of twelve paintings by one single painter (Yi Yuanji).

The second peak is created by the productivity of several artists, although most of them contribute only one gibbon painting. The majority of paintings of this peak is produced by the painter and Chan monk Muqi ($n = 32$). The clustering of gibbon painters that were active during this second peak may be underrepresented in the graph because most of the excluded paintings of unknown authorship were created in exactly this time period.

The third peak of Chinese gibbon paintings exhibits both a massive surge in the individual output of some painters as well as a drastic increase in the number of gibbon painters.

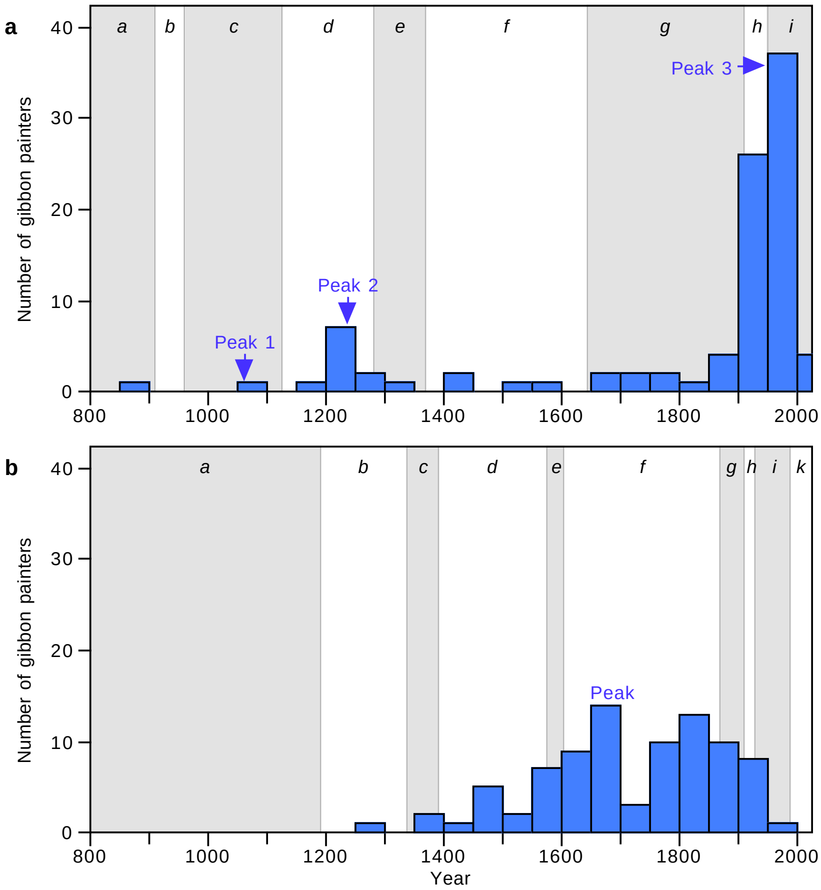

Fig. 48. Number of Chinese (a) and Japanese (b) gibbon painters versus the main activity period or midlife time of the artist. Data: All known artists until April 2008 ($n = 95$ Chinese and 86 Japanese artists). Each blue bar represents the known gibbon paintings of a time period of 50 years. Peak labels, alternating grey and white bars in the background and abbreviations as in Figs. 2 and 29, respectively. – *Anzahl identifizierter Gibbonmaler, aufgetragen gegen die Lebens- oder Aktivitätszeit der jeweiligen Künstler. Jeder blaue Balken entspricht einem Zeitraum von 50 Jahren. Datensatz: (a) 95 chinesische und (b) 86 japanische Künstler*.

The four most prolific Chinese painters (Liu Wanming, Tian Shiguang, Chen Wenxi, and Fang Chuxiong) contributed together 286 paintings, which represents about 45% of all Chinese gibbon paintings. The main activity period of each of these painters is relatively recent (20th or 21st century).

The Japanese peak in the number of gibbon paintings roughly coincides with the main activity period of the painter and Zen monk Hakuin Ekaku ($n = 9$ paintings).

The four most prolific Japanese gibbon painters are Hakuin Ekaku, Hashimoto Kansetsu, Kano Tanyu, and one of seven painters who each are represented with four paintings in this sample. Together, they contributed only 24 paintings, which represents about 16% of all Japanese gibbon paintings. The main activity period of these painters occurred in the time period from about 1575 to 1800 (Fig. 49b); only one of them (Hashimoto Kansetsu, 1883-1945, Fig. 42) had his main activity period in the 20th century.

Figure 49 suggests that the individual output of each artist is not evenly distributed in the sample. It appears as if many Chinese artists since the 20th century were specialized in painting gibbons, whereas most earlier Chinese and Japanese artists produced only few gibbon paintings each. In order to verify this statistically, the sample used for Fig. 49 was divided into three groups: (1) Chinese painters before 1900 ($n = 29$ artists), (2) Chinese painters after 1900 ($n = 66$), and (3) Japanese painters ($n = 86$). A statistical comparison of the numbers of paintings by each artist using ANOVA (and a significance threshold of 0.05) revealed a significant difference among the three groups ($df = 2$, $p < 0.004$). Scheffe's *post-hoc* test revealed a significant difference between Groups (2) and (3) ($p = 0.005$), but no significance between Groups (1) and (2), and Groups (1) and (3), respectively ($p > 0.05$ in each comparison). If the two early Chinese gibbon painters Yi Yuanji and Muqi are excluded, the comparison between Groups (1) and (2) also becomes statistically significant ($p < 0.05$). Apparently, it is Group (2) which differs most from the other groups, suggesting that the average individual output of Chinese gibbon painters may have changed (increased) around the beginning of the 20th century.

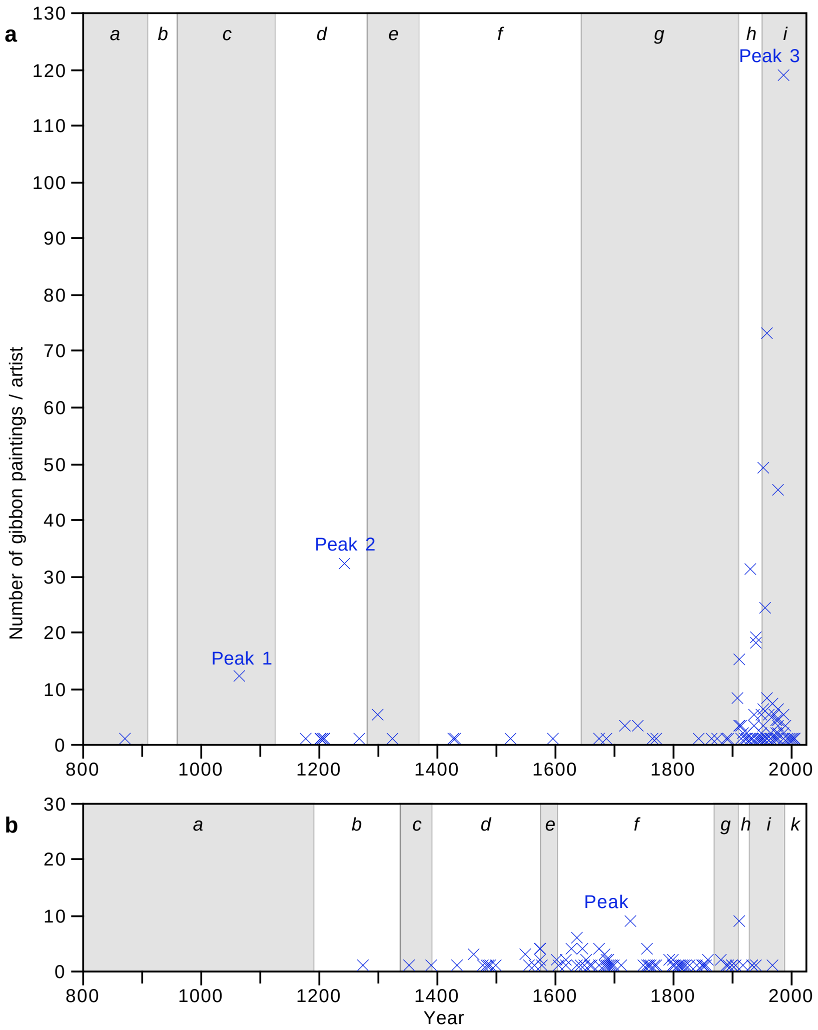

Fig. 49. Number of gibbon paintings for every Chinese (a) and Japanese (b) gibbon artist versus the main activity period or midlife time of the artist. Data: Each cross represents all known paintings of one artist until April 2008 (*n* = 95 Chinese and 86 Japanese artists). Peak labels, alternating grey and white bars in the background and abbreviations as in Figs. 2 and 29, respectively. – *Anzahl Gibbonbilder, die von jedem chinesischen und japanischen Künstler gemalt wurden, aufgetragen gegen die Lebens- oder Aktivitätszeit der jeweiligen Künstler. Jedes Kreuz entspricht einem Künstler. Datensatz: (a) 95 chinesische und (b) 86 japanische Künstler*.

Discussion and Conclusions

China

Paintings of gibbons collecting or carrying peaches, and gibbons associating with lohans (*arhats* in Sanskrit) reoccur throughout the whole history of Chinese gibbon paintings. The earliest gibbon painting found during this study already depicts a lohan who is offered peaches by a gibbon. In early Buddhism, lohans were considered as disciples who practiced and cultivated the Buddhist faith on their own. In later periods, however, they became revered as popular figures of salvation similar to bodhisattvas. In paintings, they were often situated in remote landscapes and often shown in association with certain animals and plants that played a role in overcoming the limits of ordinary life, such as gibbons and peaches (Fang Jing Pei, 2004).

The gibbon itself is associated with the wisdom of long life and the attainment of other-worldly knowledge. The peach is the divine fruit of immortality. Peach trees blossom in the early spring amid the snow, and so peaches are associated with endurance and long life. A magic grove of peach trees, which blossomed only once in three thousand years, was cultivated by the Daoist divinity the Queen Mother of the West (Xi Wang Mu) (Fang Jing Pei, 2004; Silbergeld, 1987). Eating a peach from her mythical garden was said to assure a life span of a thousand years. Paintings combining gibbons (a symbol of longevity) with peaches have a long tradition in China. Portrayed together, they represented a wish for longevity.

Even in modern China, gibbons are of continued relevance as a symbol of longevity and endurance. This is documented by the production of batteries with the brand name “Changbiyuan” (i.e. long-armed ape or gibbon) by the Kunming Battery Factory, Majie, Xijiao, Kunming, Yunnan province. The factory was established in 1956, and the batteries were still in use during my last field survey of gibbons in Yunnan Province in 2007 (Fig. 50).

Fig. 50. Batteries with the brand name "Changbiyuan" (i.e. long-armed ape or gibbon) produced by the Kunming Battery Factory, Majie (Xijiao, Kunming, Yunnan province). Photo: Thomas Geissmann. – *Batterien unter dem Markennamen "Changbiyuan" (d.h. langarmiger Affe oder Gibbon) werden auch heute noch von der Kunming-Batterie-Fabrik in Majie (Xijiao, Kunming, Provinz Yunnan) hergestellt. Dies belegt die fortdauernde Bedeutung, welche die Gibbons als Symbole für Langlebigkeit und Ausdauer in China innehaben.*

As notable change during of the 20th century, gibbon paintings began to feature increasing amounts of red colour, usually in the form of trees with red autumnal leaves. The earliest gibbon paintings of this type are dated from 1934, but as the date of most Chinese paintings is not exactly known, the preference for red colour may have started earlier. The trend is neither specific for gibbon paintings, nor to paintings of the flowers and birds genre, but was noticeable in all genres of painting.

Chinese art of the last 50 years was strongly tied to the political direction of communist China, if not an instrument of politics. Gibbons were usually painted or partially painted in ink, and ink paintings were the expressive medium of the traditionalists or artists that went into exile because of changed political situation. Before the Anti-Rightist Campaign of the year 1958, ink painting was considered an approved artistic medium which – widely unchanged and unquestioned – retained the traditional colour- and form-language. Ink painting remained welcome as long as it did not drift into surreal or abstract art. Only when artists had to fear being stigmatized as right elements or intellectuals did they change the colour palette, in which case they tended to adopt red as the dominant colour, avoiding wet black ink and, instead, inking only in grey tones. The red flag waving over China united everything. The inherent symbolism and the trick to use red as the often only bright colour for all intents and purposes served political requirements (Hesemann, 2006).

After the establishment of the People's Republic of China in 1949, the leader of the Chinese Communist party and the first Chairman of the PRC, Mao Zedong (1892-1976) had called on China's artists to subjugate their creative impulses to serve the communist party through agit-prop and other Mao-motifed works (Andrews, 1994; Hyer and Billingsley, 2005; Pomfret, 2007). Ideology was an important aspect of the arts and many artists devoted themselves to the study of the poems composed by Mao Zedong. The poems depicted the country's entrance into a new era in which people lived joyfully and had a proper livelihood. They attracted many artists of the time and played a crucial role in the content of paintings, especially in the 1950s and the 1960s; it provided those suffering artists a precious space for creation (Siu Fun-Kee, 2007). For instance, the sentence "All the mountains are blanketed in red, and forests are totally dyed" comes from Mao Zedong's poem *Chang Sha* (*To the Tune of Spring Beaming in a Garden*). It was written in 1925 and published in 1957. The cited sentence was a most welcome and many painters depicted autumnal mountains with red leaves. Overseas art historians have termed such paintings "Red landscapes" and attribute to them political meanings and characteristics of the time when China was under the rule of the "red" regime (Siu Fun-Kee, 2007). The sentenced may also have fuelled the production of paintings depicting gibbons in autumnal trees.

Most painted gibbons exhibited a black coat and a white face ring. White gibbons were depicted less often, but became more common from 1934 on, which corresponds to the time when red became a favourite colour in gibbon paintings. In the ancient Chinese concepts of colour, the colour white represents multiple things (Fang Jing Pei, 2004). In Chinese culture colours corresponded with the five primary elements, the directions and the four seasons. White was associated with metal, west, and autumn. This colour also corresponded to gold, and was the symbol for transparency, brightness, clarity, purification, fullness, justice, or punishment. Finally, white was linked to the activities of killing and destruction. White, in most cases, is the opposite colour of red (Keller, 1996; Zhou, 2006). Although gibbons occur in numerous fur colourations, purely white gibbons have not been described so far (Geissmann, 1995); the lightest gibbon fur colours are yellow or blonde. The artists' growing preference for white gibbons probably had a symbolic meaning. If the gibbon was a symbol of longevity and endurance, a white gibbon probably was a particularly pure form of the same symbol. If white was a symbol of autumn, the combination of a white gibbon with autumnal red tree foliage may have been a particularly strong association with autumn. As autumn was also the season to crusade and to execute criminals (Zhou, 2006), it is tempting to speculate that this type of paintings may also have included a political allusion.

Whereas the distribution range of the gibbons in the 10th century extended over much of China as far north as the Yellow River at the 35th parallel of latitude, Chinese gibbons lost most of their habitat in the following centuries (Van Gulik, 1967) and today occur only in few small relic populations limited to southern Yunnan, and one minuscule population each in Guangxi province and on Hainan island (Geissmann, 2007). As a result, gibbon artists had less and less access to their subjects. They had to rely increasingly on classical Song paintings in order to see what gibbons looked like. Consequently, many painted gibbons during the Ming (1368-1644) and Qing dynasties (1644-1911) began to exhibit anatomical features or positional behaviour that do not occur in gibbons. Artists who knew gibbons only from hearsay began to confuse them with macaques or other monkeys. In many secondary pictures of gibbons – drawn by artists who had not seen actual specimens – the apes are provided with small tails. Chen Wenxi (1906-1992) was awed by the lifelike quality of a print of one of Muqi's gibbon paintings (the triptych described in the Introduction section, Fig. 1) and studied it in order to emulate the painting. Chen had never seen a gibbon when he was in China, and as a result he did not realize that gibbons, unlike monkeys, have no tails. It was only much later in the late-1940s, that a foreigner pointed out this error in his painting, and corrected him (nafahub.com, 2008; Wikipedia contributors, 2008). As noted by Van Gulik (1967, p. 33), "it seems that the Chinese could not reconcile themselves to the idea that there existed a tail-less primate," but paintings of gibbons with short tails were also produced by Japanese and Korean artists that were obviously unfamiliar with actual gibbons.

In the 20th century, however, some gibbon painters began to keep gibbons as pets in order to benefit from the inspiration provided by watching them. For instance, Zhang Daqian (1899-1983) obtained his first gibbon in 1945, while he was still living in China, from a friend in Singapore. Zhang was said to have raised about thirty gibbons during his lifetime, and when he lived on a large estate in Brazil "during the 1950s and 1960s, the space and favourable climate made it possible for him to rear ten gibbons, the largest group he ever had" (Fu and Stuart, 1991, p. 162). Similarly, Chen Wenxi (1906-1992) began to specialize in gibbon paintings after he settled in Singapore in 1948. He is reported saying: "I used to admire the paintings of gibbons of Muqi, especially the way he executed the furs, so delicate and so true to life, and I concluded that these results were possible only by close and prolonged watching of real-life models. So in Singapore, when I saw one day a gibbon, I bought it to be my model. This was followed by half a dozen other gibbons, which I bought at different times – black, white, grey, all kinds, which I have incorporated into a number of my works" (nafahub.com, 2008). Examples of Chen Wenxi's gibbon paintings are shown in Figs. 22-23.

This study shows that the production rates of gibbon paintings in China and Japan exhibit different trends and fluctuations.

In China, gibbon paintings are found from the 9th century until present. This is much earlier than suggested by previous publications, which usually assume that gibbon painting as a genre developed during the Northern Song dynasty (960-1126) (Bai, 1999; Van Gulik, 1968). Furthermore, gibbons depicted on belt buckles and relief bricks date back to at least the Han dynasty (206 BC-AD 220), with one silvery jewel in the shape of a long-armed primate not reliably identifiable as a gibbon dating back to the Warring States period (475-221 BC). Artefacts such these suggest that gibbons already played an important role in Chinese culture well before the Song dynasty. Finally, references to gibbons are plentiful in all literary forms from the Han dynasty (202 BC-AD 221) onwards (Van Gulik, 1967; Lovell, 1981). This evidence suggests that paintings of gibbons, too, may have been produced much earlier than the 9th century, but none were preserved until the present time.

At least three marked peaks in the production rate of gibbon paintings can be discerned in China. It is generally accepted that an increased preference for animal and flower paintings occurred during the Song period, and it has been pointed out that "Gibbons had been a staple subject of the Song Academy, and many examples of the genre by the Song masters were in the imperial collection" (Barnhart, 1996, p. 339). The data collected for this study suggests, however, that gibbon painting during the Song period falls into two distinct periods, each with its own distinct peak. The first peak occurred in 1050-1075 and is related to the successful career of the Northern Song painter Yi Yuanji (active in the 1060s), who is generally identified as the first painter to specialize in depicting gibbons (Bai Qianshen, 1999; Lovell, 1981; Van Gulik, 1968). This assessment may or may not be correct, but Yi Yuanji was certainly the first to achieve fame for his depictions of gibbons (Barnhart *et al.*, 1997). He was so famous as a gibbon painter, that the Emperor Yingzong (reigned 1064-1068) commissioned him to paint *One Hundred Gibbons* on the walls of one of the halls in the Imperial Palace, but he died before finishing the painting (Van Gulik, 1967). The imperial collection in the early 12th century reportedly contained 245 works by Yi Yuanji, of which 114 were gibbon and monkey paintings (Lovell, 1981, p. 60). The latter number differs considerably from the 11 gibbon paintings attributed to Yi Yuanji (plus a few monkey paintings) that were seen during this study, that the historical losses of artworks must have been immense.

To judge by the highly diverse styles of these paintings, however, it seems questionable whether all paintings attributed to Yi Yuanji were made by the same artist. The effortless virtuosity with which the painter populates a landscape with rather naturalistically painted gibbons in Fig. 8 differs considerably from the ornamental construction of the gibbon family shown in Fig. 9. It should also be noted that attributions of paintings to artists were and still are a big problem in Chinese art history in general and in the Northern Song period in particular (Hesemann, 2006, p. 142f). As pointed out by Lovell (1981), it was a common occurrence in the history of Chinese painting that the name of the most famous artist working with a certain subject, theme or style became synonymous with that subject, and the majority of subsequent works in the genre automatically acquired an attribution to the artist. “Very few authentic works by Yi Yuanji survive today but many a gibbon painting purports to be from his hand” (Lovell, 1981, p. 60). Furthermore, copying paintings of old masters was a common practice throughout much of China’s history (Unverzagt, 2005; Wong, 1962), which might also account for some of the stylistic diversity of paintings attributed to one artist (such as Yi Yuanji). If this interpretation is correct, some of the paintings may have been created slightly after (or even before) Yi Yuanji’s activity period. As a result, the first peak in the number of gibbon paintings/time would be flatter and less conspicuous than shown in Fig. 2.

The second peak in the number of gibbon paintings/time occurred in the period from 1200 to 1325. Although works by several artists are included in this peak, most of the paintings (69%) from that time are attributed to Muqi (c.1210-1325). Thumbnails of many of these gibbon paintings are shown in Gotoh Museum (1996). In some of these gibbons, the fur is painted to look thick and soft, in others, it has a more bristle appearance; some gibbons have prominent fluffy ears, others don’t, and some gibbons exhibit thick, furry limbs, whereas others have extremely lean and unrealistically long limbs (a feature that was developed only much later by Japanese gibbon painters). Although 31 paintings examined during this study are attributed to Muqi, their high stylistic diversity makes it unlikely that all of them were made by the same artist. If some of these paintings postdate Muqi, the second peak might exhibit a more bell-shaped form than shown in Fig. 2.

A gibbon painting that looks very much as if painted by Muqi is shown in Fig. 21. This painting was copied from an existing painting attributed to Muqi and is a well documented example of a painting that was made as a forgery. Zhang Daqian (1899-1983) painted it in the style of a Southern Song dynasty painting, in the style of the artists Liang Kai and Muqi (Fu and Stuart, 1991; von Spee, 2007). He even “aged” and intentionally wrinkled the paper to make it look old, and he asked the calligrapher and artist Pu Xin-yu (= Pu Ru, 1896-1963) to write some inscriptions and a poem (not shown in the figure). Zhang Daqian was not only a versatile and highly productive painter and collector-dealer, but probably the greatest Chinese painting forger of all time. His forgeries included some of the greatest names in all of Chinese painting and even anonymous Buddhist works (Whitfield, 1993).

Peaks one and two can be linked to the productive gibbon painting career of two famous Chinese artists. After the end of their career, no further artists became known for being specialised in painting gibbons until the 20th century, suggesting that the absence of peaks in the period from the 14th to 18th century is a real finding and not an artefact of either the sampling effort invested in this study or the differential preservation of paintings in certain time periods.

The most pronounced peak in the number of gibbon paintings/time, however, is the third one (Fig. 2). This sudden and huge increase in the production of gibbon paintings started early during the 20th century. Why did painting gibbons suddenly become so attractive?

One could argue that the art of the 20th century is simply better documented or preserved than that of earlier periods. However, the preservation probability or documentation quality of paintings should asymptotically approach zero the further one goes back in time. Abrupt changes in the number of paintings should not occur according to this hypothesis. The increased production of gibbon art must, therefore, have been influenced by other aspects (e.g. patronage of particular rulers, historical events, economy, etc.).

An alternative explanation could be that landscape painting appears to have lost some of its significance starting with the 18th century (but especially during the 20th century), whereas other genres such as figure and animal paintings became more dominant (Andrews, 1994; Blunden and Elvin, 1983, p. 173; Hesemann, 2006, p. 239; C. von Spee, pers. comm.). If this interpretation is correct, it would be compatible with the results of this study, but the original question “Why did gibbon paintings suddenly increase in dominance?”, would then need to be replaced with the question: “Why did figure and animal paintings suddenly increase in dominance?”.

As a third explanation, it is possible that a single influential painter like Zhang Daqian (1899-1983) may have “re-animated” gibbon painting (C. von Spee, pers. comm.). This artist had a special preference for painting gibbons (Fu and Stuart, 1991; von Spee, 2007). If this interpretation is correct, it would mean that Zhang Daqian had considerable influence on the artists of his time. In fact, more than 40 artists began to paint gibbons between 1900 und 1975. It is unclear, however, whether Zhang Daqian could have had such an influential role during the 50 years he spent in China. Born in 1899 in Sichuan, he was committed to an artistic career by the age of 20 and spent some time in Shanghai as an art student. His retreat from Peking with the Japanese invasion in 1937 led to life in Sichuan, interrupted by two and a half years at the frontier site of Dunhuang (1941-43). With the advent of the People’s Republic he left China in 1949, never to return (Edwards, 1992).

As shown in Fig. 48, not only the number of Chinese gibbon paintings but also the number of Chinese painters that specialized in gibbon paintings increased dramatically (and statistically significantly) during the 20th century. However, the occurrence of this peak in gibbon paintings is not the sole result of these specialists’ combined activity. Figure 49 also shows an equally dramatic increase in the number of non-specialists (i.e. painters who produced only one or two gibbon paintings each) which also contributed to the peak.

In any case, a relatively sudden increase in the dominance of gibbon paintings occurred during the 19th century. The reasons for this increase are not well understood and will require further study. The rise in gibbon paintings/time during the 20th century appears to coincide roughly with the Republic of China-period (1911-1949). It has been well documented that various artistic styles and techniques experienced rapid changes (and sometimes reversals) in acceptance during the 20th century in China, especially during the years between 1949 and 1979, when the Chinese Communist Party (CCP) succeeded in eradicating most of those of which it disapproved (Andrews, 1990; 1994). The communist party put into effect a radical program of reform under the strict control of the party commissars, who decided what kind of art should be made and which artists would be permitted to work. In the early 1950s, the styles derived from traditional Chinese painting and from the École des Beaux-Arts were declared elitist and corrupt and would be replaced by Socialist Realism. A brief period of liberalisation during the Hundred Flower Movement in 1956 was followed by a brutal crackdown of intellectual critics of the regime under the Anti-Rightist Campaign of 1957. When Mao launched the Great Leap Forward in 1958, the mass collectivization of peasants into people's communes and the forced development of rural industrial production resulted in an economic catastrophe and an epic famine (Fong, 2001, p. 206). As economic disasters piled up and the national morale sagged, a revived interest and respect for the traditional art occurred in the early 1960s. It was nowhere more apparent than in painting where once again political content was abandoned.

By late 1963, Jiang Qing, the third wife of Mao Zedong, had begun to rise in power and to exert control over the arts. As the economy recovered from mistakes of the Great Leap Forward and the communist party recovered its shaken self-confidence, the lenience towards apolitical art began to disappear. In 1966, Mao unleashed the Cultural Revolution, a disastrous campaign to heighten the revolutionary goals of the Communist party (Fong, 2001, p. 206f). The Cultural Revolution policies of Jiang Qing and the other members of the Gang of Four completely dominated art, imbuing it with an unprecedented political saturation. Art for art's sake was condemned and only art that idealized the workers, peasants, and the military was sanctioned. It was characterized by “red” in both colour and content. Artists, writers and intellectuals were “purged”, sent into the countryside or to prisons. By the end of 1966, rampaging Red Guards went on a massive campaign to destroy religious structures and institutions, destroy “counterrevolutionary” art and architecture, and burn ancient scrolls and books, thus obliterating a large part of China's cultural heritage (Anonymous, 2005). The Cultural Revolution ended in 1976 with the death of Mao Zedong and the arrest of the Gang of Four in the same year.

None of the cultural events and changes described above appears to explain how and why gibbon painting as a genre received such a formidable boost during this time period.

Another change that must have affected not only working conditions of artists but also their outlook on art itself occurred at the end of the Cold War in 1979, when the Chinese government formalized a new policy of openness to the West (Andrews, 1994). During the first 70 years of the 20th century, western art turned its back to realism and – with several experiments – passed the period of Modern Art. “At the end of the Cold War in the 1970s, when China opened itself to the world anew, […] Chinese artists were surprised to discover the extremely disharmonic relation between their art and the modern tendencies of the international art. As a result, realist painting, which had developed in China for nearly one century, lost its importance for the artists, especially those of the younger generation. Therefore, in 1979, at the beginning of the Contemporary Chinese art, we are still looking at a sinking culture, like at the beginning of the 20th century” (Li, 2005). One would expect that a new policy which initiated a re-orientation of artists and to the rise of the Contemporary Chinese art may also have initiated a decline of the gibbon painting genre. However, no such trend can be discerned from the data collected for this study (Fig. 2).

This study documents for the first time that the gibbon painting genre survived all political and social troubles and changes that occurred during the 20th century. Not only did the genre survive, it actually began to thrive during this period, possible more than ever before, and it appears to continue to thrive today. This is unexpected. Books that document the development of Chinese art during the last 50 years often focus on its strong ties to the political direction of communist China, and exhibitions of Contemporary Chinese art in the west tend to show art which exhibits at least a trace of protest against the political situation (Andrews, 1994; Fibicher and Frehner, 2005; Hesemann, 2006; Hyer and Billingsley, 2005). For instance “Revolutionary Realism”, the dominant art style in the time period of 1949 to 1979, was foremost a political tool, and the political message of most paintings was clearly in the foreground (Hesemann, 2006, p. 242). In contrast, gibbon paintings show very little evidence of a political context. The use of red or vermillion accents mentioned above, for instance in the foliage of trees, is usually interpreted as a political statement, but its use was independent of gibbon art, and paintings with red trees became quite popular (e.g. Siu Fun-Kee, 2007). Of course, Chinese artists are famous throughout the centuries for hiding political or other messages in the form of subtle symbolic allusions and rebuses (e.g. Bai Qianshen, 1999), but if any political meanings are hidden in gibbon paintings of the 20th century, these meanings, like the gibbon paintings of that time period themselves, appear to have remained unstudied so far. Gibbon paintings represent an essentially traditionalist genre. How and why it started to thrive during the 20th century and still continues to do so is unclear and deserves further study.

Japan

Japanese painting was influenced by Chinese painting while still pursuing its own path. This resulted in different results and developments than that found on the mainland and gives Japanese art in general, and Japanese gibbon art in particular, an interest all its own. A comparison of the gibbon paintings from China and Japan reveals that the historical development of the genre took a different course in the two countries.

In Japan, the earliest gibbon paintings found during this study date from the 14th century, which is again earlier than the 15th or 16th century reported in previous publications (Cunningham, 1991, p. 46; Van Gulik, 1968, p. 97). When discussing a Japanese gibbon painting, Woodson and Mellott (1994, p. 85) reported that "curious monkeys were closely observed and depicted in Chinese paintings as early as the thirteenth century, and in Japanese paintings in the fourteenth century". Unfortunately, these authors regarded and identified all primates as "monkeys" (even gibbons, which are not monkeys, but apes). This makes it impossible to decide whether the authors are referring to gibbons or monkeys in the sentence quoted above. Mislabelling "monkeys" as "gibbons" or "apes" and vice versa is not only extremely common in Western texts (e.g. English titles of paintings as shown in Figs. 31, 33, 37, 40, 41), but, unfortunately, occurs in Eastern texts as well.

Japanese gibbon paintings were produced until the first half of the 20th century, with a peak in the number of paintings at around the mid-Edo period (first half of the 18th century).

It is generally believed that the most influential gibbon painter for the development of Japanese gibbon art was the Chinese Zen monk Muqi (c.1210-1275). Muqi's works were brought back to Japan by Japanese Zen monks who had visited China (Woodson and Mellott, 1994) somewhere between the 13th century (Van Gulik, 1968, p. 97) and the 15th century (Cunningham, 1991, p. 46). Muqi's paintings had such a powerful impact on Japanese ink painting in general, and gibbon painting in particular, that the art of pivotal Japanese painters like Hasegawa Tohaku is virtually incomprehensible without taking it into account (Kuroda, 1996).

Zen Buddhism itself was formally established in Japan at the end of the 12th and the beginning of the 13th century (Brinker *et al.*, 1996, p. 12), or in the late 13th or early 14th century (Woodson and Mellott, 1994).

As mentioned above, the occurrence of, and preference for, gibbon paintings in Japan appears to be closely linked to the import of Chan (Japanese: Zen) Buddhism from China to Japan. This interpretation is supported by the observation that the majority of the Japanese gibbon paintings depict the theme of the "Gibbon reaching for the moon" or "Gibbon reaching for the reflection of the moon in the water", a favourite theme in Zen Buddhism both satirizing human folly (reaching into the water in a vain effort to capture the reflection of the moon served as an example of senseless greed and the desire to possess things that cannot be used) and symbolizing the search for enlightenment (Cunningham, 1991, p. 110; Woodson and Mellott, 1994, p. 85). In contrast, only few Chinese gibbon paintings are devoted to this theme (for instance two attributed to the Chan monk Muqi).

As speciality of Zen pictures, often only those elements are depicted which are relevant for understanding the theme of the painting. In many gibbon paintings, for instance, the gibbon is seen hanging from a branch, but the water and the reflection of the moon are not visible. In some cases, the gibbon is not even reaching down towards a potential water surface, but up towards the moon (which may or may not be visible in the painting). The viewer himself is supposed to supplement the picture by meditating about the topic of the painting and, by doing so, getting approaching enlightenment.

A fairly common variant of the theme of the "Gibbon reaching for the moon" in Japan depicts a gibbon chain. Suspended from one gibbon supported by a tree branch, numerous gibbons form a long chain, each clinging to the arm, hand or foot of another, the lowest of the group trying to reach for the reflection of the moon in the water. As correctly pointed out by Van Gulik (1967, p. 7), gibbons are not known to deliberately collaborate using this method for reaching from a high place an object down on the ground.

Gibbon holding, offering or gathering peaches are depicted only rarely (only one example was found during this study). This theme is more common in Chinese and Korean gibbon paintings. It alludes to Chinese legends about the fruit of immortality and the Daoist Queen Mother of the West.

Conspicuous large folding screens (*byobu*) and sliding doors (*fusuma*) depicting gibbons (Figs. 31, 32, 37) first appeared in the Muromachi period (1392-1573) and became more common during the Momoyama epoch (1573-1603) and well into early Edo period (1603-1868). Originating in China, the first screens used in Japan, from the seventh to the eighth century, came from China and Korea. Later, screens were made in Japan. The most common format is the pair of six-panel folding screens, each screen measuring about one and a half meters high and about three and a half meters wide. The use of a gold foil background for painted screens came into extensive use during the sixteenth century and covers the surface of some of the most magnificent screens (Klein and Wheelwright, 1984a, b; Yonemura, 1993).

In a famous gibbon screen by Hasegawa Tohaku (1539-1610), the use of gold helps to create a dream-like scene, as if taken from another, better world (Fig. 32). Screens were part of a uniquely Japanese expression of a monumental style that flourished during the Momoyama epoch (1573-1603) (Cunningham, 1991). During the Momoyama epoch, warlords built tall, fortified castles, with small windows. The owners decorated the larger wall areas of the dim interior spaces with sliding doors and folding screens painted with auspicious themes (Woodson and Mellot, 1994). As these large paintings served to impress rivals and allowed the owner to display his wealth and status, painters were forced to create a new, monumental style of art. The colour that these artists particularly favoured was gold, and compositions done in ink and rich pigments on gold-leaf backgrounds became the most characteristic works of Momoyama art. It has been hypothesized that this extremely free use of gold leaf, which had been known but seldom employed by artists of the Muromachi period, was partly dictated by the need for greater illumination in the dimly lit reception halls of Momoyama castles (Varley, 2000). The stability and prosperity of the Edo period (1603-1868) led to the emergence of new patrons from the merchant class. This situation encouraged artistic innovation and the continued creation of screens and other art embellished with gold and silver (Fig. 35).

In contrast to Chinese gibbon art, Japanese paintings often show gibbons as fluffy hairballs with big round heads and small faces. These infantile features, or “babyness” factors were referred to originally by Lorenz as the “*Kindchen-Schema*” (cited in Eibl-Eibesfeldt, 1989). As another trend, many Japanese artists depict gibbons with impossibly long arms, especially during the Edo (1603-1868) and Meiji periods (1868-1912).

During the same periods, the theme of “the gibbon reaching for the reflection of the moon in the water” became so popular in Japan that all kinds of objects were decorated with this design (ranging from dishes, perfume boxes to swords).

The decline of gibbon painting as a genre in Japan probably was initiated by, and began soon after, the radical changes that occurred at the beginning of the Meiji period in 1868. At this time, the Tokugawa-Shogunate was abolished and replaced by the Meiji imperator, and Japan was opened to foreign citizens (Dunn, 2006a). Furthermore, this was “a time when Buddhism had suffered persecution after the radical change to the new Meiji regime” (Onishi, 1993). As Japanese gibbon paintings appear to be almost completely confined to Zen-Buddhistic contexts, the genre probably began to lose ground at the same time as Buddhism.

To judge by the absolute number of gibbon paintings, it would appear that Japan produced more gibbon paintings than China during the time period from the 17th to the 19th centuries. However, such a comparison makes sense only if the preservation of paintings were similar in both countries. Whether this assumption is valid is questionable.

Gibbons do not naturally occur in Japan, in contrast to their originally vast distribution in China (e.g. Geissmann, 1995; Groves, 1970). Although McShea Ewen (1998) reported that “The Japanese had a special fondness for gibbons, as they were native to Japan,” this incorrect information probably results from a misquote of Woodson and Mellott (1994, p. 85): “The Japanese had a special fondness for monkeys, as they were native to Japan.” As mentioned above, Woodson and Mellott erroneously regarded and identified all primates (including gibbons) as monkeys. It serves as a good example of how incorrect terminology, once created, continues to confuse later authors. As a result, every statement on “monkeys”, “gibbons” or “apes” in Chinese, Japanese and Korean art should be regarded with caution. Often, the meaning of a text is unclear until one sees the paintings the author is referring to.

Korea

In contrast to Chinese and Japanese art, Korean art survives in much smaller quantities and has been less widely studied. Chinese, Mongol, Manchu, and Japanese armies have attacked and looted Korea at various times in the country’s history. That so few historical records, artworks, or architectural monuments survived from before the late sixteenth century is largely a result of the destruction wrought by these incursions (Hammer and Smith, 2001).

Because of its geographical position, Korea frequently functioned as a conduit between China and Japan for ideas and beliefs, material culture and technologies (Dunn, 2006b; Hammer and Smith, 2001).

The numerous Buddhist pilgrims who travelled from Korea to China and India introduced types and styles of Buddhist images from China and India, enriched the iconographic repertoire and contributed to the common international style that characterized Buddhist sculptures of the Unified Silla dynasty (AD 668-935) and the Koryô dynasty (AD 918-1392). The Koryô court and aristocracy were the fervent patrons of Buddhist art (Cambon and Carroll, 2005, p. 182), and the majority of Korea’s most important surviving art treasures were inspired by the practice of Buddhism (Hammer and Smith, 2001). Sôn is the Korean version of the meditative Chan Buddhism (Japanese: Zen), which developed in China between the sixth and seventh centuries. A form of Chan Buddhism was transmitted to Korea perhaps as early as the seventh century, reportedly by a Korean monk who studied in China. After the twelfth century, Sôn became the dominant form of Buddhist practice in Korea (Hammer and Smith, 2001).

During the early Yi dynasty (AD 1392-1910), Confucianism became the state philosophy (Cambon and Carroll, 2005; Dunn, 2006b). The Neo-Confucian revolution experienced in the 16th century was broad and profound in its effects, and the results were devastating. The Korean version of Neo-Confucianism that became the dominant Yi ideology by the end of the 16th century was an inherently intolerant doctrine, and its followers were quick to reject and suppress other teachings, including Buddhism (Cambon and Carroll, 2005, p. 69).

Although Buddhism continued to be popular among commoners and in the countryside, with intermittent royal tolerance, it never again had the artistic pre-eminence that it once enjoyed, and the production of Buddhist-related works was openly discouraged (Cambon and Carroll, 2005, pp. 11, 182). Korean painting during the Yi period was more influenced by Chinese artists of the Southern Song (AD 1127-1279) academy tradition than those of contemporary Chinese scholar-painters.

Only few gibbon paintings from Korea were found during this study. Although this is difficult to quantify, it appears that gibbon (and monkey) paintings were always less common there than in China and Japan. Neither gibbons nor monkeys naturally occur in Korea. This, and the suppression of Buddhist-related art during the Yi dynasty (AD 1392-1910), may explain the apparent rarity of paintings of these animals in Korea, but conclusions drawn from this small sample must be regarded with caution.

The available Korean gibbon paintings rarely appear to exhibit a clear Buddhist context. The Buddhist parable of the gibbon reaching for the moon's reflection in the water, which is illustrated so often in Japanese gibbon paintings, does not occur in the Korean sample. Only one painting of the 19th century can be placed in a Buddhist context as it combines the gibbon or gibbon-like animal with a Buddhist monk. In contrast, several paintings depict gibbons holding or gathering peaches (Daoist symbols of longevity).

No gibbon paintings older than about 1550 were found during this study. This may be either due to the small sample size of Korean gibbon paintings, or because so few of the paintings before the fifteenth century survived (Hammer and Smith, 2001, p. 61). The growing popularity of both Sôn Buddhism and of Chinese paintings from the Southern Song era influenced the art production in Korea during the Yi dynasty (1392-1910) (Hammer and Smith, 2001). Both developments may have been factors in the introduction of the gibbon painting genre to the country.

Korean artists were probably inspired by Chinese paintings of these animals, and most appear to have been unfamiliar with the animals themselves. Many of the painted gibbons exhibit facial expressions, short tails, body proportions, or positional behaviour that do not occur in real gibbons, suggesting that many Korean artists had less access to the classical Chinese gibbon paintings than Japanese artists. For instance, one painting by Yun Duseo (1668-1718) shows a gibbon hanging from a branch, but not suspended by its hands, but by its axilla (Fig. 45). This awkward position is not known to be adopted by living gibbons. It is unclear when depicting gibbons in this position was invented, but gibbons in similar positions were painted by Chinese artists such as Hua Yan (1682-1756), Zhang Shanzi (1882-1940), Zhang Daqian (1899-1983), Mu Lingfei (1913-1997), and Tian Shiguang (1916-1999), as well as Japanese artists such as Kano Koi (c.1569-1636).

During Japanese domination (1910-1945), Korea was not only modernised, but Korean traditional painting was excluded from academic studies, Western art and art education was introduced into society, and Korean artists were indoctrinated in Japanese-style painting (Ahn Hwi-joon, 1994). These difficult times for Korean painting may also have had a damaging impact on gibbon painting. The most recent Korean gibbon painting found during this study dates from 1940, suggesting that the genre may have lost some or most of its already moderate relevance in modern Korea.

Dating of Events

As shown above, gibbon paintings in both China and Japan are older than assumed in previous publications. Similar dating problems occur in paleontological studies, which often date the origin of an extinct group of organisms based on the earliest preserved fossil representant of that group. Although paleontology appears to be only distantly related to cultural history, specialists of both disciplines have to deal with quite similar problems. Gaps in the preservation of cultural relicts and gaps in the fossil record pose similar scientific challenges to the evaluation of the data. Therefore, scientists working in one of the two disciplines may benefit from the methodology of the other. As discussed by Martin (1993), direct dating of phylogenetic origins is confronted with two problems: (1) If a group is documented by few fossils only, the oldest fossil representant of this group is with a high probability considerably younger than the real origin of its group. (2) Trends in the fossil representation can produce additional errors. The same rationale applies to direct dating of the origin for cultural products. (i) If only few items of product are preserved, the oldest preserved item is with a high probability considerably younger than the real origin of this type of product. (ii) Trends in the preservation can produce additional errors. As a result, direct datings tend to produce origins that are considerably too young, especially when a high percentage of the material to be dated has not been preserved.

It is known that Chinese painting flourished as early as the Zhou period (11th ct. BC - 221 BC) and that emperors of the Han dynasty (206 BC - AD 220) who were connoisseurs of art owned picture collections (Cohn, 1942). Yet, because paintings on silk or paper get destroyed easily, complete or partial destruction of both large imperial and private collections with thousands or tenthousands of paintings due to fire and water occurred periodically

(Unverzagt, 2005). As a result, relatively few paintings predating the Song period (960-1279) are preserved today, giving us only a vague idea of the painting of the early periods (Münsterberg, 1968; Pope *et al.*, 1961-1962; Unverzagt, 2005). In the numerous invasions, changes of dynasties and revolts the palaces of the great with their priceless contents were the first victims of destruction (Cohn, 1942). Similar losses also characterize the history of Korean art and, possibly to a lesser degree, Japanese art (Hammer and Smith, 2001; Münsterberg, 1968; Priest, 1958; K. Epprecht, pers. comm.), suggesting that the origin of gibbon paintings as a genre may have a much earlier date, at least in China and Korea, than suggested by the earliest gibbon paintings found during this study.

This hypothesis is also supported by the observation that objects decorated with gibbon designs or sculpted in gibbon-shapes are known from periods as early as the late Eastern Zhou period (4th-3rd century BC). They predate the oldest recorded gibbon painting (9th century) by more than a thousand years. Because many of these objects are made of metal, they are less easily destroyed than paintings on silk or paper.

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Zusammenfassung

Gibbonbilder in China, Japan, and Korea: geschichtliche Verbreitung, Produktionshäufigkeit und Entstehungskontext

Gibbons, die kleinen Menschenaffen der Familie Hylobatidae, belegten und belegen eine wichtige Nische in der chinesischen Kultur, und für lange Zeit taten sie das auch in der japanischen und koreanischen Kultur. Dies manifestiert sich unter anderem in der häufigen Darstellung dieser Tiere in den bildenden Künsten. Dies ist die erste Studie, in der die Produktion von Gibbonbildern dieser Länder in verschiedenen geschichtlichen Zeitabschnitten mengenmässig erfasst und verglichen wird. Insgesamt wurden 818 Gibbonbilder erfasst. Die Untersuchung zeigt, dass die frühesten Gibbonbilder deutlich älter sind als in einigen früheren Veröffentlichungen angegeben. Dies gilt sowohl für China (vor der Song-Dynastie) als auch für Japan (vor der Momoyama-Periode). Zusätzlich sorgen die kleinen Stichprobenzahlen früher asiatischer Gemälde dafür, dass das Genre der Gibbonbilder in jedem der untersuchten Länder ein noch deutlich früheres Entstehungsdatum gehabt haben dürfte, als es durch die frühesten in dieser Studie gefundenen Bilder angezeigt wird.

Uspründlich entwickelte sich das Genre in China, breitete sich dann aber auch in die Nachbarländer Japan und Korea aus, obwohl dort Gibbons nie heimisch waren und die Künstler daher wenig eigene Kenntnisse von den dargestellten Menschenaffen hatten. In China wurden Gibbons in ganz verschiedenen Kontexten und Funktionen dargestellt. Dazu gehören unter anderem Vorstellungen von Gibbons als Bindeglieder zwischen Mensch und Natur, als Wesen, die fähig sind, menschliche Gestalt anzunehmen oder hunderte von Jahren alt zu werden, und als sinnbildliche Träger erstrebenswerter menschlicher Attribute. Gibbons werden dargestellt als in Bilderrätsel (Rebus) eingekleidete Glückwünsche zum Bestehen von Prüfungen oder Wünsche für hohe Amtspositionen, als ursprünglich daoistisches Konzept eines Überbringers von Früchten, deren Genuss Langlebigkeit verheisst, oder in der buddhistische Parabel vom “Greifen nach dem Spiegelbild des Mondes” als Sinnbild von menschlichem Streben nach dem Unmöglichen oder Sinnlosen. In Japan wurde des Genre der Gibbonmalerei von Zen-Buddhisten eingeführt, und von Anfang an ist die überwiegende Mehrzahl der Gibbonbilder in Japan dem buddhistischen Motiv “Greifen nach dem

Spiegelbild des Mondes” gewidmet. Stilistisch jedoch haben sich die chinesischen und japanischen Gibbonbilder sehr schnell voneinander entfernt.

In den koreanischen Gibbonbildern fehlt das Motiv vom “Greifen nach dem Spiegelbild des Mondes”, aber die geringe Grösse der koreanischen Stichprobe lässt wenig verallgemeinernde Aussagen zu.

Die Herstellungshäufigkeit von Gibbonbildern pro Zeiteinheit weist starke, bisher nicht dokumentierte Schwankungen auf. Im Zeitraum von 1525 bis 1900, als Gibbonbilder in China zwar regelmässig, aber nicht häufig gemalt wurden, war die Beliebtheit des Genres in Japan (gemessen an der Zahl der erhaltenen Bilder) sogar konsistent höher als im Ursprungsland der Gibbonbilder.

Der dramatischste Anstieg der Produktionsrate erfolgte jedoch in China während des 20. Jahrhunderts. Während das Genre der Gibbonbilder zu diesem Zeitpunkt in Japan (und vermutlich in Korea) am Erlöschen war, erlebte China einen bisher nicht belegten und anscheinend in dieser Grössenordnung erstmaligen Anstieg sowohl in der Zahl der Künstler, welche solche Bilder malten, als auch in der hohen Zahl solcher Gibbonbilder, die von einigen Spezialisten unter diesen Künstlern hergestellt wurden. Die Ursachen für diese Veränderungen sind noch unerforscht, aber einige mögliche Gründe werden hier diskutiert. Schliesslich dokumentiert diese Studie auch Änderungen im Stil und im Kontext der Gibbondarstellungen, die in verschiedenen historischen Zeitabschnitten auftraten, und diskutiert auch für diese die mögliche Ursachen.

The gibbons of Pu Mat National Park in Vietnam

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The white-cheeked gibbons at Pu Mat National Park in Vietnam have not been studied previously. In July of 2007 I visited the park for a project on the vocal diversity and systematics of crested gibbons (genus *Nomascus*). During a survey covering about 58 km^2, or approximately 6% of the whole park (911.13 km^2), I was able to hear two groups of gibbons and make sound-recordings of these groups. My finding that the gibbons survive in Pu Mat National Park at extremely low densities (at least in my survey area) can be regarded as ominous news. Gibbons from this area are generally identified as southern white-cheeked crested gibbons (*Nomascus siki*), but their calls differ from more southern populations (for instance those of the Bach Ma National Park) that are usually believed to be of the same taxon.

The Pu Mat National Park

Pu Mat National Park is located in north-central Vietnam (Fig. 1), about 200 km southwest of the capital, Hanoi, within the Nghe An province at the border of Laos. The western boundary of the park forms part of the Lao-Vietnamese border. The geographical coordinates of the park are from N 18°46′ to 19°12′ and from E 104°24′ to 104°56′ spreading in three districts of Tương Dương, Con Cuông and Anh Sơn of Nghệ An Province.

Pu Mat may be Vietnam's best-studied national park in that a detailed inventory of the biodiversity of this remote pocket of highly intact forest has been established (Grieser Johns, ed. 2000). Located in the north of the Greater Annamites ecoregion, the steep terrain as well as the size and remoteness of this area have protected the wildlife of Pu Mat from the extensive exploitation found in many other areas of Vietnam (Fig.2). Without this intact habitat, species such as Asian elephant, tiger and saola would probably no longer be found in Pu Mat. Reportedly, the elephant population of Pu Mat is particularly important given the dwindling populations across the ecoregion, particularly in Vietnam (World Wildlife Fund, 2007). They are said to cross into and out of the national park across the international border with Lao P.D.R. However, with the ever increasing population of the region, this wildlife is coming under increasing threat (Grieser Johns, ed., 2000). The National Park is working to safeguard this biodiversity while also ensuring the livelihoods of local communities. Pu Mat NP is one of the remaining areas in Vietnam, which still supports gibbons (Geissmann *et al.*, 2000; Nguyen Minh Tam and Vo Huy Thong, 1998). However, no systematic gibbon surveys have been carried out in this forest, so far.

Fig. 1. Map showing the location of the Pu Mat, Phong Nha–Ke Bang and Bach Ma National Parks in Vietnam. – *Die Karte zeigt die Lage der drei Nationalparks Pu Mat, Phong Nha–Ke Bang und Bach Ma in Vietnam.*

Fig. 2. A first impression of the steep terrain of the Pu Mat National Park, as seen from the entrance of the park. Photo: Julia Ruppell. – *Vom Eingang des Pu Mat Nationalparks erhält man einen ersten Eindruck von der Steilheit des Geländes.*

Elevations at the nature reserve range between 100 and 1,841 m, although 90% of the nature reserve is under 1,000 m in elevation, lower than many other national parks in Vietnam. The highest points in the nature reserve are found in the south, along the mountain ridge that forms the international border between Vietnam and Laos. A series of steep-sided valleys run perpendicular to this ridge, forming a series of smaller north-south ridges (Kemp *et al.*, 1995). The steep terrain in most parts of the nature reserve has been an obstacle to extensive clearance of forest (Grieser Johns, ed., 2000). The nature reserve is drained by four main rivers: the Khe Thoi, Khe Bu, Khe Choang and Khe Khang (Kemp *et al.*, 1995). All four rivers feed the Ca river (Song Ca), which runs from west to east, through a wide valley to the north of the nature reserve.

Vietnam supports several gibbon species all of which are crested gibbons (genus *Nomascus*). The gibbons in central Vietnam are of particular interest. They have traditionally been identified as southern white-cheeked crested gibbons (*N. siki* or *N. leucogenys siki*). Recent research suggests that more than one taxon may be included under this name and that central Vietnam is part of a larger area where the “identity” of the gibbons is uncertain (Ruppell, 2007a; 2007b; Geissmann *et al.*, 2000; Konrad and Geissmann, 2006). Gibbon calls (usually termed songs) exhibit species-specific characteristics and can be used to assess phylogenetic relationships among the species and maybe even among populations (Dallmann and Geissmann, in prep.; Geissmann, 2002a, b; Konrad and Geissmann, 2006; Keith *et al.*, in prep.).

This study was part of an on-going project on the vocal diversity and systematics of crested gibbons undertaken by the Gibbon Research Lab. at Zurich University, Switzerland. The goal of my study was to tape-record the songs of the gibbons in Pu Mat NP in order to learn more about their affinities (through comparison with recordings collected at other localities), and to obtain preliminary information on the population density of these gibbons. This report deals with the assessment of the current distribution and status of the poorly known gibbons in this national park obtained during my research.

Surveying the gibbons

The locations of gibbon groups, and the density and size of a gibbon population can be estimated based on their vocalizations. The gibbon population size in the park has not been estimated before. Because no detailed gibbon surveys had been previously carried out in the area where I conducted my data collection, I generally had no knowledge of the gibbon density and the distribution of individuals, groups and their territories. Local people and park staff provided a good source of information and were consulted as to whether gibbons had been heard in the area in recent times. Once at such a reported gibbon locality in the field, a camp and listening post were set up. Once gibbons were heard, the listening post was moved in the direction of the gibbon group during subsequent mornings, in order to obtain clearer recordings. Once a good set of recordings for a group was collected, I attempted to locate a different group in the same locality. Because gibbons live in small family groups and because mated crested gibbons normally produce duet songs but not solo songs, a group can be defined when a male and female duet is recorded for one location. Each duet that was heard on a given day was recorded and the direction of the group song was noted using a GPS and compass. This process ensures that the number of gibbon groups heard each day can be differentiated from each other during data analysis.

The trek to find gibbons began with several days of travel from Hanoi to Nghe An province and Vinh city. From Vinh city my assistant and I travelled by bus to Pu Mat NP headquarters through which the park can be entered. We met with the national park staff in order to arrange permits for entering and camping in the park. I was assigned one ranger, one former-hunter, and one local inhabitant of the park who were to stay with me and my assistant during my stay in the park (Fig. 3).

Fig. 3. Research team. – Zum Team dieser Freilandstudie gehörten ein Feldassistent, ein Park-Ranger und lokale Führer.

Human inhabitants of the park are of the Danlai ethnic group. Although they spoke no English, they were quite helpful in pointing me in the direction of the "*vuon*" (gibbon). No main service road cuts through Pu Mat National Park. We therefore spent several days boating and hiking from the buffer zone into the core zone of the park. I focused on these areas for locating gibbons as we made our way deeper into the park (Fig. 4). Our survey area was located in the SE of the park, in an area called Khe Bong. This area was chosen because park rangers reported that gibbons had been heard there most recently. They also mentioned the NW part of the park where gibbons were reported in 2000 (Fig. 4). However the rangers said that it was extremely difficult to work there because of the terrain.

It was not until we reached the Khe Bong area that we heard gibbons. During the following mornings we climbed up to various peaks in order to be in an optimal position to detect gibbon songs (Fig. 5). Every morning, we began hiking in the darkness of 04:00 hr, in order to arrive on our listening posts before dawn, when the gibbons start to sing. As there were no trails, our path was obstructed by saw palmettos, bamboo and ferns. The only way up the steep peaks was through an almost vertical climb using branches and roots like ladder rungs. My assistants blazed the trail with machetes clearing the brush and saw palmettos.

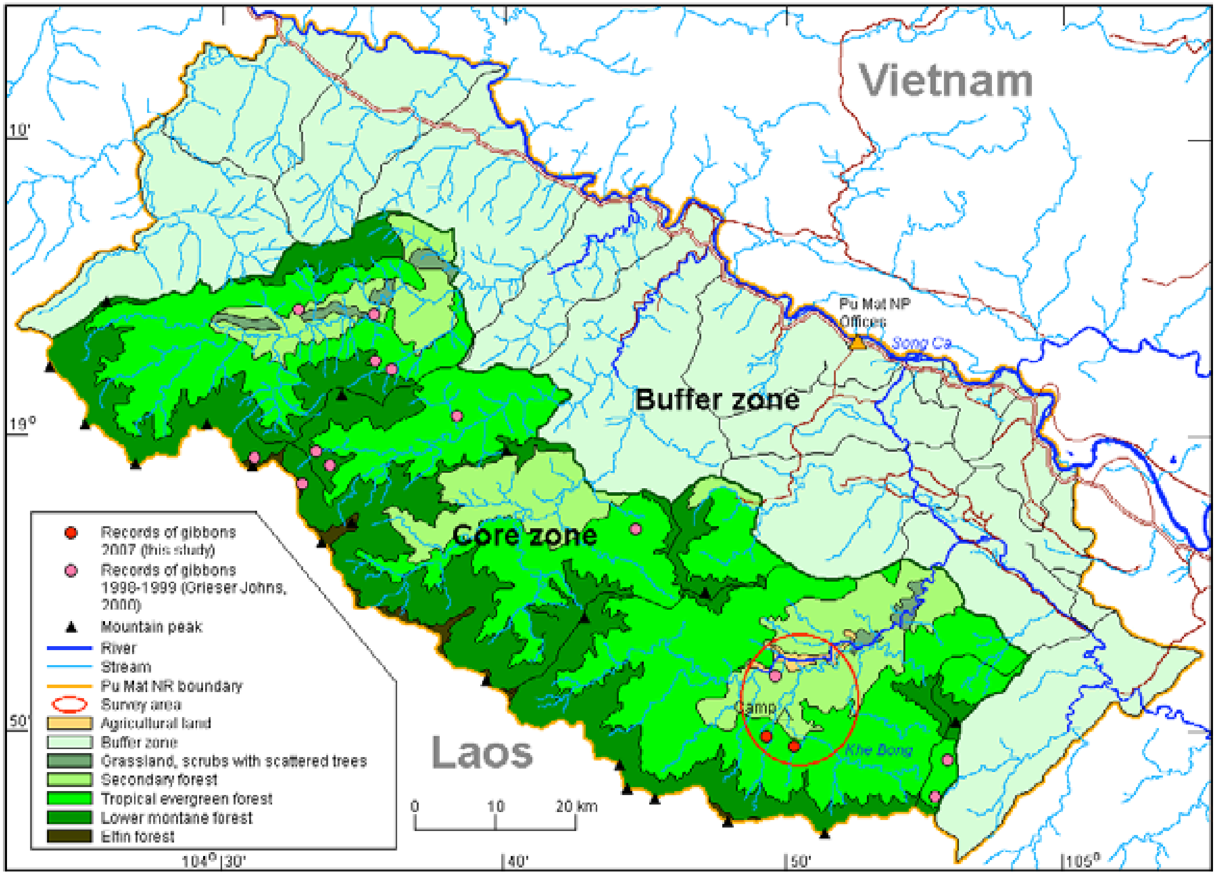

Fig. 4. Map of the gibbon survey area (red circle) in Pu Mat NP. – Karte des Pu Mat Nationalparks. Der rote Kreis bezeichnet die Lage des Untersuchungsgebietes (survey area).

Fig. 5. At the listening post. Photo: Julia Ruppell. – *Auf dem Hörposten auf einem Hügel im Nationalpark, bereit, die Gesänge der Gibbons zu orten und auf Tonband aufzunehmen*.

On the first morning that we heard gibbons it took us an hour to reach our chosen listening post. I immediately set up my recording equipment and told everyone to be silent. That morning, two groups were heard from the listening post. Both groups were heard coming from the same direction (west towards Lao P.D.R).

During this study we tried to locate and record as many gibbons as possible. Every day, we arrived on our chosen listening post between 04:00 and 04:30 hrs and stayed there until 11:30 hr. During afternoons, we made survey walks in the forest. During twenty consecutive days of monitoring, a total of only six song bouts were recorded. I heard less than one song bout per day (average ± standard deviation: 0.3 ± 0.25 song bouts per day; range: 0-2 song bouts). Gibbons often started singing a few minutes before sunrise (i.e. 05:37 hr local time). The average starting time of song bouts was 05:49 hr. No song started earlier than 05:20 hr and none after 06:39 hr. Of the few songs that I heard the duration was very short (average ± standard deviation: 4.53 ± 1.32 minutes, range: 3-5 minutes). This duration appears very short compared to the gibbons of Phong Nha-Ke Bang NP (Ruppell, 2007a) where song bouts had an average duration of 13.2 ± 2.8 minutes (range 6-18 minutes).

Songs of two groups were effectively tape-recorded. No other groups were heard. Therefore my estimate for the area between the Pu Mat NP office and Khe Bong area is that there are at least two groups (with at least four individuals) living in this area. I heard no young gibbons join in the great calls of the adult gibbons.

Assuming that a gibbon song carries about 1 km in the forest, an area of roughly 3 km^2 could be monitored with one listening post and about 15 km^2 with five listening posts that are separated at least 2 km from each other. This very tentative method suggests that gibbon density was extremely low (0.03 groups/km^2) compared to other areas that were surveyed using the same method. For example in Phong Nha-Ke Bang the gibbon density was about 0.7 groups/km^2 (Ruppell, 2007a). In Bach Ma (Thua Thien Hue Province) of central Vietnam the gibbon density was about 1.3 groups/km^2 (Geissmann *et al.*, 2007). In the Nam Kan area of Laos the gibbon density was 2.2 groups/km^2 (Geissmann, 2007). An average gibbon group may not sing every day and remain silent for up to five consecutive days. Therefore, it is possible that some groups in the survey area remained undetected during this short study.

There are various other places in Pu Mat NP where gibbons have been reported to have been heard within the park during the 1990's. They are reviewed in Geissmann *et al.* (2000), and the localities mapped by Grieser Johns (2000) are shown in Fig. 4. Additional surveys until 2002 were summarized by Nguyen Thanh Nhan (2004), who concluded that the gibbon was "the primate easiest to observe in Pu Mat National Park". However, there has been little recent evidence, aside from anecdotal, to suggest that gibbons are still found in other areas.

No other mammal species were seen during this survey. Several other primate species are reported to exist in the park such as the red-shanked douc langur (*Pygathrix nemaeus*), eastern spectacled leaf monkey (*Trachypithecus crepusculus*), stump-tailed macaque (*Macaca arctoides*), Assamese macaque (*M. assamensis*), long-tailed macaque (*M. fascicularis*), rhesus macaque (*M. mulatta*), pig-tailed macaque (*M. nemestrina*), Bengal slow loris (*Nyticebus bengalensis*), and pygmy loris (*N. pygmaeus*) (Nguyen Thanh Nhan, 2004). Of these, the long-tailed macaque is probably an introduced species that does not naturally occur in Pu Mat NP.

Discussion

Beginning my trip, I had no idea what I would find. I knew there was a possibility of searching for days and hearing no gibbons. Earlier surveys carried out in Pu Mat NP during the 1990s (summarized in Geissmann *et al.*, 2000) only heard few (one to four) gibbon groups at the surveyed localities.

The survey area is within the distribution area of what is currently known as the southern white-cheeked crested gibbon (*Nomascus siki*). Though the call characteristics of the gibbon songs I heard differ from those recorded by Thomas Geissmann at Bach Ma NP, i.e. from a forest area located further to the south (Fig. 1) and very close to the type locality of *N. siki* (Konrad and Geissmann, 2006; Geissmann *et al.*, 2007; Tallents *et al.*, 2001). This conflicting evidence documents that the systematics of the crested gibbons require further study (Ruppell, 2007a, b). We simply do not know how large the gibbon population is, and a large part of the forest remains to be surveyed.

Conservation Issues

Currently, the biggest threat to biodiversity at Pu Mat NP is hunting, which is widespread at the site and represents a particular threat to populations of primates (Cao Van Sung and Le Quy An, 1998; Cao Van Sung, undated). All of the rangers that I spoke to said that there is still some hunting that continues. However, they believe that now the majority of the problem comes from traps, not guns. We noticed several traps during our survey (Fig. 6). Despite the presence of large areas of relatively undisturbed habitat, hunting threatens the populations of many mammal species and some bird species at Pu Mat.

Fig. 6. Animal trap. Photo: Julia Ruppell. – Im Wald fanden sich oft Wildtier-Fallen wie die im Bild gezeigte.

Of large concern are villages of local Danlai ethnic groups within the park where hunting is not monitored. The Danlai have inhabited the area for hundreds of years. The human population density appeared high inside the park (as compared to Phong Nha-Ke Bang NP (Ruppell, 2007a). For example, about 5-10 human inhabitants were seen on a daily basis in all of the gibbon survey area (Fig. 7). More than 800 people live inside the protected area of Pu Mat NP. According to rangers, before 2004 almost every family had a gun for hunting. This may explain the low density of primates. After 2004 Pu Mat NP staff collected all of the guns from local people. However, legal passage is allowed between Vietnam and Lao P.D.R. for commerce and family relations as the local Danlai have relatives in Lao. This increases the risk of guns being brought back into the park if not carefully monitored. The Danlai only learn up to the primary level of school in their village. Most people do not continue any education after what is considered a third grade education. Perhaps an improved education system would enable understanding of their potential impact on endangered animals.

According to rangers and local people, there used to be primates everywhere in Pu Mat NP a few years ago. I was told by a long term resident that he used to see gibbons almost every day until around four years ago. This is a striking contrast to our study as we did not encounter any mammals. On the other hand, there appeared to be no previous information on the occurrence of gibbons in the Khe Bong area where we found them. According to local people, the gibbon groups had recently moved into the area.

The results of the earlier surveys indicate that at least one critically threatened mammal, the red-shanked douc langur, is so rare that it was believed extinct in Pu Mat NP after the survey work in the 1998-1999 (Grieser Johns, ed., 2000), although its continued occurrence there was confirmed in 2002 (Nguyen Thanh Nhan, 2004).

Fig. 7. Danlai hut and clearing. Photo: Julia Ruppell. – Eine Hütte der lokalen Danlai Bevölkerungsgruppe in einem abgeholzten Waldabschnitt.

The gibbon was considered “the primate easiest to observe in Pu Mat National Park” in a summary of survey work until 2002 (Nguyen Thanh Nhan, 2004), but this comparison does not say anything about the absolute abundance of the species.

Because of the high quality of its forest, Pu Mat should be one of the best gibbon areas in Vietnam. The density, however, appears to be lower than in similar habitat in Laos (Timmins *et al.*, 1998, cited in Geissmann *et al.*, 2000, p. 75), suggesting that the gibbon population suffers heavily from hunting. This also corresponds to the findings of this study. As shown in the Results section above, the gibbon density determined during this survey is lower than that of other *Nomascus* localities that were surveyed using the same method. An unsustainable gibbon population compounded with local hunting could lead to the eradication of all gibbons from the park.

In addition to hunting, illegal timber extraction is a major threat to biodiversity, and again occurs largely in response to commercial demand (Cao Van Sung and Le Quy An, 1998). Natural resources are also under great pressure from the expanding surrounding population. Large-scale illegal timber extraction is taking place along the main river valleys in the nature reserve. This activity is changing the composition of the forest. Widespread rattan and orchid collection is also depleting populations of these plants within the nature reserve (Grieser Johns, ed., 2000). The greatest threat to populations of reptile and amphibian species within the nature reserve is collection by local communities. The majority of these animals enter the wildlife trade. Unless nature reserve management regulations and wildlife trade laws are strictly enforced, populations of turtles, monitor lizards and pythons at Pu Mat are threatened with extinction (Blazeby *et al.*, 1999).

Lastly, almost nothing is known on the gibbons in the park. The recent distribution, density and population size of the gibbons at Pu Mat NP are unknown (aside from this study) and no directed conservation efforts are being performed in the park for gibbons at this time.

In summary, much of the gibbon news reported here is sobering but the situation is not hopeless. There are still gibbons surviving in the wild of Vietnam and with our help they may endure to keep on singing their beautiful morning songs.

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Zusammenfassung

Die Gibbons des Pu Mat Nationalparks in Vietnam

Obwohl der Pu Mat Nationalpark wohl einer der best-untersuchten Nationalparks in Vietnam ist, wurden die dort lebenden Weisswangen-Schopfgibbons bisher noch nicht wissenschaftlich erforscht. Der Park ist einer der letzten Lebensräume für Vietnams verbleibende Gibbonpopulationen.

Die Gibbons im zentralen Teil des Landes, in welchem auch der Nationalpark liegt, sind von besonderem Interesse, weil ihre Verwandtschaftsverhältnisse noch ungeklärt sind. Da sich die Gesänge der Gibbons zwischen den Arten unterscheiden, können Tonaufnahmen der Gesänge dazu verwendet werden, solche verwandtschaftlichen Beziehungen zu erforschen. Die Gibbons von Zentralvietnam wurden bisher als südliche Weisswangen-Schopfgibbons (*Nomascus siki*) bezeichnet; allerdings unterscheiden sich ihre Gesänge von anderen, weiter südlich lebenden Populationen, die bisher zur selben Art gerechnet wurden (zum Beispiel die Gibbons im Bach Ma Nationalpark).

Zusätzlich können die Gesänge auch dazu verwendet werden, eine Bestandesaufnahme der Gibbons durchzuführen. Im Juli 2007 habe ich deshalb den Pu Mat Nationalpark besucht, um dort einen Teil eines Projekts über die Gesänge und die Systematik der Schopfgibbons (Gattung *Nomascus*) durchzuführen. Das von mir untersuchte Gebiet umfasste ca. 58 km^2, was etwa 6% der gesamten Parkfläche entspricht. Um die Bestandesaufnahme durchzuführen, wurden auf Hügeln so genannte Hörposten eingerichtet. Von dieser erhöhten Lage aus hatten wir optimale Voraussetzungen, um die Gibbongesänge zu hören, die Tiere zu lokalisieren, sowie Tonaufnahmen der Gesänge zu machen.

Morgens um 04:00 Uhr verliessen wir jeweils das Camp, um vor Sonnenaufgang am jeweiligen Hörposten anzukommen. Meistens begannen die Gibbons wenige Minuten vor Sonnenaufgang mit ihren melodischen Gesängen. Schofpgibbons leben in kleinen Familiengruppen, in denen das Männchen gemeinsam mit dem Weibchen im Duett singt. Während 20 Untersuchungstagen konnten wir allerdings nur zwei Gibbongruppen hören und lediglich sechs Gibbongesänge aufnehmen.

Diese Studie zeigt, dass es offensichtlich nur noch sehr wenige Gibbons im untersuchten Gebiet gibt und dass die Verbreitungsdichte der Gibbons im Pu Mat Nationalpark geringer ist als in anderen Schopfgibbon-Gebieten, in denen die gleichen Untersuchungsmethoden angewendet wurden. Die grösste Gefahr für die Gibbons im Pu Mat Nationalpark ist die illegale Jagd, aber auch die massive Abholzung trägt zur Ausrottung bei. Es wäre sinnvoll, die lokale Bevölkerungsgruppe der Danlai, die auch im Nationalpark leben, mit gezielter Aufklärungsarbeit auf die Auswirkungen der Jagd und der Abholzung aufmerksam zu machen. Obwohl es in diesem Nationalpark noch Gibbons gibt, ist ihre Situation kritisch. Es bedarf dringender Schutzbemühungen, damit in Pu Mat auch in Zukunft noch die wunderschönen Gesänge der Gibbons zu hören sein werden.

Observations on paternal care in a captive family of white-handed gibbons (*Hylobates lar*)

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Among the small apes only siamang males are known to display extensive paternal caretaking behaviour. We observed parental behaviour in a captive family group of white handed-gibbons (*Hylobates lar*). Our results suggest that paternal involvement in infant care may be more variable than previously believed. The pattern of dealing with the infant (type of care, time budget, and initiating interactions) exhibited gender differences.

Introduction

Mammals living in social monogamy often exhibit high levels of male parental care (Kleiman, 1977). Although the small apes or gibbons typically live in social monogamy (Chivers, 2001), the amount of male parental care exhibited by gibbons is believed to exhibit a sharp dichotomy: Whereas siamang (*Symphalangus syndactylus*) fathers were observed to carry their offspring during the second year (e.g. Chivers, 1972, 1974, 2001), infants of other gibbon species were carried by their mothers (e.g. Gittins and Raemaekers, 1980, p. 70; Wright, 1990). It is generally believed that there is no evidence to indicate that gibbon males – siamangs excepted – exhibit any measurable amount of direct paternal care (Reichard, 2003, p. 190). Nevertheless, there is some anecdotal evidence that male infant carrying occurs at least in some wild and captive gibbon groups other than siamangs (Fischer and Geissmann, 1990; McCann, 1933). In addition, there are some field observations on *Hylobates muelleri* and *H. pileatus* males that spent more time playing with, and grooming, infants than their mates did (Leighton, 1987), and with a study on a juvenile captive male pileated gibbon (Geissmann, 1997) displaying helping behaviour.

Here we report on paternal behaviour observed in a captive family of white-handed gibbon (*H. lar*) at the Debrecen Zoo (Hungary).

Animals and methods

The study group consisted of a 19-year-old female, called Lenocska; a 13-year-old male, called Jerry, and their male offspring, called Sanyi aged 5 months at the beginning of the study. They were kept in a combined indoor/outdoor cage with the indoor cage consisting of two separate smaller cages between which they could move freely. Both parents were captive born, had been mated for 5 years and had produced a previous male offspring that was no longer housed with the family.

The gibbons were observed and video-recorded at intervals ranging from one to three months from 11:00 h a.m. to 15:00 h p.m., through 13 months. The study took place between December 1999 and February 2000. The behavioural measures taken from the video recordings were duration of social interactions involving one of the parents and the offspring, and the initiation of dyadic social interactions by any group member. The following social interactions were quantified between father and son: carrying, playing, sharing food, and grooming. In order to obtain further information about parental motivation, we introduced two types of interventions: (1) preferential feeding of selected individuals to check patterns of food sharing, and (2) alternating separation of one of the parents.

Preferential feeding of the parents occurred when the infant was 8, 10, and 13 months old. Preferential feeding of the infant occurred when it was 13 months old. This time a piece of preferred food was given by one of us (ZC or MU) directly to one of the individuals as they approached us. Preferential feeding was repeated 8 times for the father, 3 times for the infant and twice for the mother.

Alternating separation of one of the parents occurred when the infant was 17 months old. Separation was carried out when one of the parents remained alone in one of the indoor cages by closing the door that was usually open between the two cages. When separated, group members could hear but not see each other. Separation events had a duration of 10 min in both cases, with 60 minutes in between.

Results

During the study period both parents provided parental care to the infant. The mother exhibited common maternal behaviour such as carrying,

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* Deceased 2004 – Greatly missed by all who knew her

suckling, grooming and food sharing. Behaviour here referred to as male care was identical to that provided by the mother, except suckling (Fig. 1).

At the beginning of the study, the percentage of time of social interactions involving mother and son was 51% of the observation time, decreasing to 12% by the end. The father's time spent in dyadic interaction with the infant decreased from 12% to 0.6% from the 5th to the 13th month of the infant's life, but increased and even exceeded maternal dyadic interactions during months 15 and 17 (Fig. 2).

The predominant male behaviour was playing (Fig. 1b) throughout the whole study period. Play involved chasing, pulling the arms and legs of the infant, slapping, embracing and mock biting. The male never took the infant directly from the mother, but usually picked it up when it was left alone. Play occurred less frequently between the adult male and female, and was never observed between the mother and her son, although the infant made attempts to involve her in the play.

Play bouts were mostly initiated by the male (84%) (Fig. 3), and often occurred despite the reluctance of the infant (especially in months 5 and 6). Sometimes play became too harsh and the infant began to squeal, upon which the mother would retrieve the infant from the father. When the mother was startled because of an unusual or loud voice she also picked up the infant immediately. The father was never observed doing so.

Fig. 1. Interactions between father and son (video stills). Left: The infant held by his father. Right: Play between father and son. – *Interaktionen zwischen Vater und Sohn (Videobilder). Links: Das Jungtier wird vom Vater gehalten. Rechts: Der Vater und das Jungtier beim Spielen*.

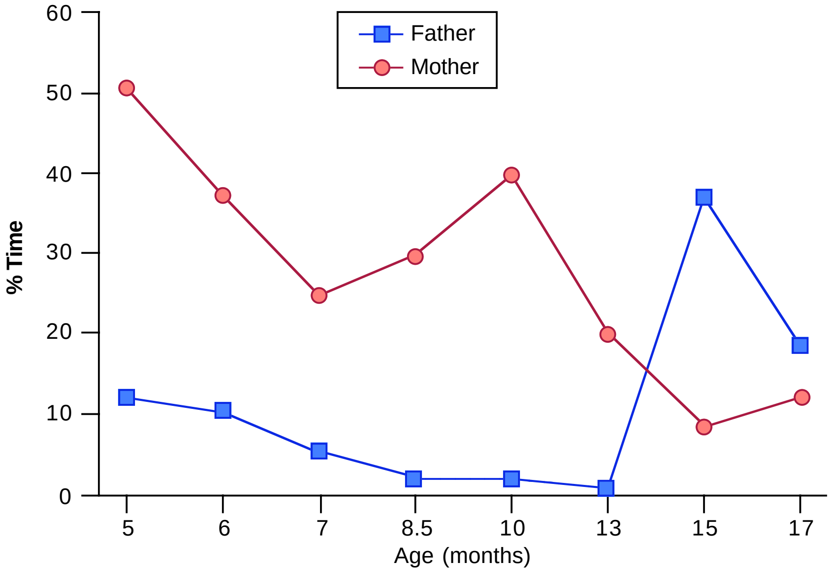

Fig. 2. Time percentages of social interactions between the infant and either parent. – *Anteil der Beobachtungszeit (in Prozent), während dem soziale Interaktionen zwischen dem Jungtier und einem Elternteil stattgefunden haben (rot: Vater, blau: Mutter).*

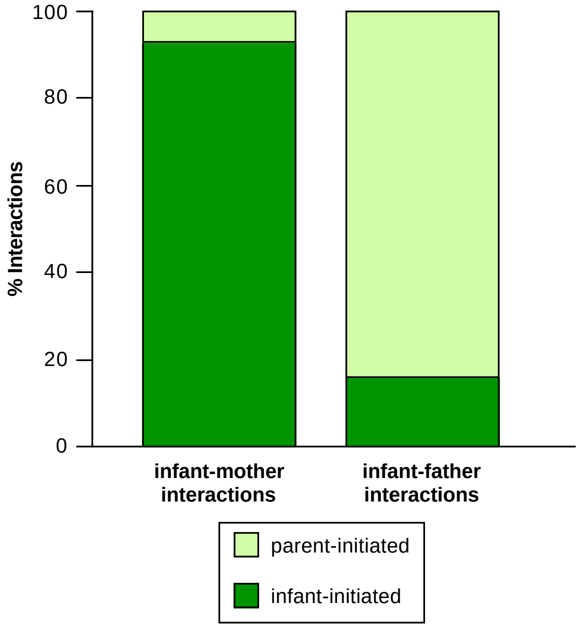

Fig. 3. Percentages of father-, mother- and infant-initiated interactions. – Anteil sozialer Interaktionen (in Prozent), die entweder vom Vater, von der Mutter oder vom Kind angeregt wurden. Links: Muter-Kind-, rechts: Vater-Kind-Interaktionen. Heller Anteil: Eltern-initiiert, dunkler Anteil: vom Jungtier initiiert.

Maternal infant carrying decreased during the study but was not quantified. As the mother-infant interactions mostly consisted of carrying and suckling, the time she spent carrying the infant probably was closely correlated to the total time of her social interactions with the infant, which is shown in Fig. 2.

We observed the infant carried by his father only in months 5 and 6 (Fig. 4). The father sharing food with, and grooming, the infant was much less frequently observed: food sharing was observed twice when the infant was six months old. The father grooming the infant was observed only once when the infant was 15 months old.

Interactions between the mother and the offspring were predominantly initiated by the offspring (93%) (Fig. 3) by approach vocalisation, which evoked an immediate maternal response in every case. The male was never observed to respond to this signal. During feeding sessions, the infant was generally eating food alone or from his mother's hand, a behaviour that generally met with no resistance from the mother.

When a preferred piece of food was given by one of us directly to the young in the presence of its parents, on two of the three occasions the mother let the infant approach us to take the food and then took it away from him. On both occasions when the mother was given the food she began to eat it and then let the infant eat of it too. Each time the father was given the food he dipped it in water for some seconds before eating it seemingly in order to soften it. On the eight occasions when the father was given the preferred food he once let the mother take it away from him. On another occasion the mother tried to get the food but she did not succeed. On a third occasion the mother, who was just carrying the infant, noticed that the father got the food, and ran to him in an attempt to obtain it. The infant also showed signs of wanting the food. At that moment the father broke the food into two pieces and put one piece near the infant who picked it up immediately and ran away with it.

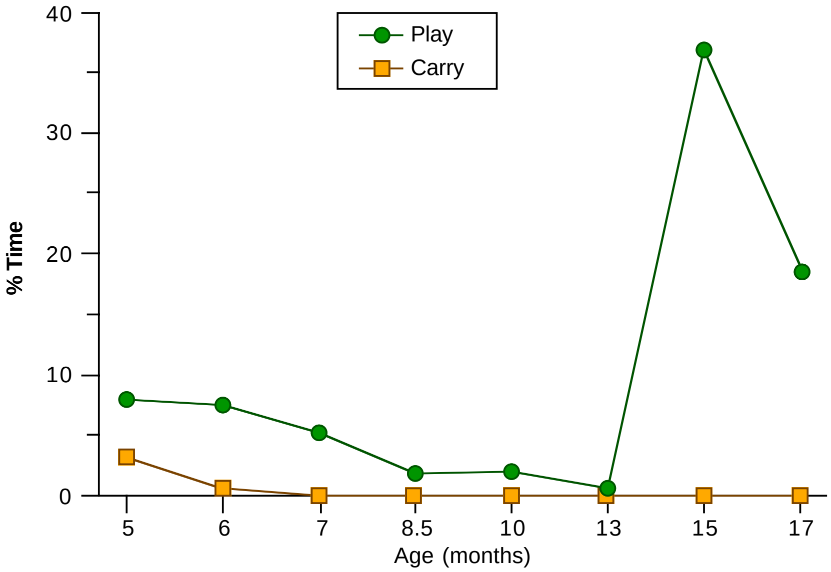

Fig. 4. Time percentages of paternal infant-carrying and playing with the infant. – *Anteil der Zeit (in Prozent), während dem das Jungtier getragen wurde (grün) und während dem mit dem Kind gespielt wurde (gelb).*

When the male was separated from the group, the mother held the infant, and every group member was relatively quiet and voiceless, although the male repeatedly went to the door. At the end of the 10 minutes of separation the mother carrying the infant immediately moved back to the other cage to the father. When the female was separated from the group every individual became excited, as evidenced by interruption of normal behaviour and squealing by the infant. The isolated mother was highly restless, repeatedly went to the door or crouched in front of it. The father also went to the door frequently and made attempts to make visual contact with the female through a small gap near the closed door. The infant also made such attempts. In this situation the infant showed signs of wanting to be carried by the father, but he did not do so. His attention was directed exclusively to the female. When the door was opened again the mother immediately ran to the infant and picked it up.

Discussion

Except for siamangs, gibbon males are usually described as not showing any measurable degree of paternal care. Here we report sustained bi-parental care in a family group of white-handed gibbons. The male studied by us showed great interest in the infant, spent a substantial amount of time playing with and carrying it and shared food with it. Caretakers reported that the male attempted to do so already in the first month of the infant's life. Two years earlier we had observed the male behave similarly toward his earlier offspring as well.

Male and female parental behaviour differed in the present study. While the father's predominant behaviour was playing, the mother did not play at all with the infant. On the contrary, the mother spent substantial time grooming the infant but only once was the father observed doing so. Although the male's interactions with the infant included virtually all elements of maternal care, there was a marked complementarity between the adults in the manner of initiating interaction with the infant. Interactions between mother and son were predominantly initiated by the infant, thus presumably reflecting the infant's needs. In contrast, interactions between father and son were mostly initiated by the parent. While the comfort-giving behaviours (carrying, protecting) were largely carried out by the female, behaviours requiring more tolerance (such as playing and active food sharing) were displayed by the father. In the preferential feeding trials the mother's behaviour was also assertive rather than tolerant. A similar observation of greater male tolerance is available on a New World monogamous species, *Callicebus moloch* (Mendoza and Mason, 1986). Previous studies on wild gibbons also report that the male's contribution to play behaviour in some species (Leighton, 1987) and food sharing in white-handed gibbons (Nettelbeck, 1998) was more pronounced than the female's part. These and our own findings provide evidence for the role differentiation in parental care in small apes.

In siamangs, the father's infant-carrying increases as the mother's infant-carrying decreases. Basically, he takes over for her during much of the infant's second year of life (Chivers, 1974). The function of the behaviour presumably is that the mother is relieved of a part of her care-giving burden when both the weight and the thirst of the infant are increasing. In contrast to the published data on siamangs, the comparatively moderate amount of infant-carrying provided by the male white-handed gibbon observed by us was highest at the beginning of our study, which is also believed to be the time when the infant-carrying provided by the mother was highest. It is possible that our study male was most inclined in paternal behaviour when the infant was "new", and that his infant-carrying may have decreased because the "novelty effect" was wearing off. Although the amount and temporal development of his paternal care do not appear to be closely related to what has been observed in siamangs, it is tempting to speculate that his disposition to provide active care for the infant may resemble the primitive condition from which the derived state of active paternal care in siamangs evolved.

Acknowledgements

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Zusammenfassung

Beobachtungen zur väterlichen Jungenpflege bei einer Zoofamilie von Weisshandgibbons (*Hylobates lar*)

Bei monogamen Säugetieren beteiligen sich die Männchen oftmals an der Jungenaufzucht. Bei den kleinen und monogam lebenden Menschenaffen ist die intensive väterliche Jungenpflege nur von den Siamangs (*Symphalangus syndactylus*) bekannt. Es wurde bisher angenommen, dass sich bei anderen Gibbonarten das Männchen kaum aktiv an der Jungenaufzucht beteiligt.

In dieser Studie wurde die Jungenpflege bei einer Zoofamilie von Weisshandgibbons (*Hylobates lar*) im Zoo von Debrecen (Ungarn) untersucht. Die Gruppe bestand aus einem 19-jährigen Weibchen, einem 13-jährigen Männchen und deren Sohn, der zu Beginn der Studie fünf Monate alt war. Die Daten wurden während 13 Monaten mittels Verhaltens-Beobachtungen und Videoaufnahmen erhoben. Es wurde unter anderem ermittelt, wie lange soziale Interaktionen zwischen einem Elternteil und dem Jungtier dauerten und welches Indivdiuum jeweils für den Beginn dieser Interaktionen verantwortlich war.

Die Resultate zeigen, dass sich sowohl Mutter als auch Vater an der Jungenpflege beteiligten. Gegen den Schluss der Studie hat sich das Männchen sogar häufiger mit dem Jungtier abgegeben als das Weibchen. Es zeigten sich auch geschlechtsspezifische Unterschiede in der Art, wie Mutter oder Vater sich mit dem Jungtier abgaben. Der Vater dieser Zoogruppe zeigte grosses Interesse am Jungtier, spielte oft mit ihm, trug es gelegentlich herum oder teilte Nahrung mit ihm. Die Mutter kümmerte sich dagegen vor allem um das Wohlbefinden des Jungen und verbrachte viel Zeit damit, das Jungtier zu groomen (soziale Fellpflege). Soziale Interaktionen zwischen Mutter und Kind wurden vor allem vom Kind angeregt, während die Interaktionen zwischen Vater und Kind vor allem vom Vater initiiert wurden. Die in dieser Studie beobachtete Jungenfürsorge des Vaters zeigt, dass bei Gibbons die väterliche Beteiligung an der Jungenaufzucht variabler ist als bisher angenommen.

Intergroup conflict in captive siamangs (*Symphalangus syndactylus*)

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In this study, I describe the increase in territorial behaviour of siamangs kept in two adjacent cages after the formation of a new pair. The formation of a new pair resulted in a significant increase of a form of inter-group agonistic behaviour ("arm-pulling"), which occurred exclusively among animals of the same sex. The increase in conflicts cannot be fully explained by the simple increase in the number of these territorial animals, but appears to be directly influenced by the formation of a new pair.

Introduction

In wild gibbons (Hylobatidae), conflicts may occur when two neighbouring groups come close together near the boundary separating their territories. During this time, males typically sit or hang and stare at each other from exposed positions in trees. Occasionally, they swiftly chase each other with vigorous movement. Females usually remain in the background but may vocalize and groom their male mates (Gittins and Raemaekers, 1980; Leighton, 1987). Disputes last from a few minutes to over two hours and about 40 minutes (Gittins, 1984) and may be accompanied by more or less intense calling by the male or by all group members. Territorial disputes are relatively rare in most gibbon populations, with rates varying between populations and over time from once every two days to as low as once a month (Leighton, 1987). Inter-group conflicts in wild siamangs (*Symphalangus syndactylus*) have been described by Chivers (1974). They are basically similar to disputes in other gibbon species but appear to be more rare (Brockelman and Srikosamatara, 1984).

Zoos only occasionally keep several gibbon groups of the same species in direct sight of each other, because this may increase rates of abnormal behaviour and heighten intra-group aggression (Ibscher, 1964). As a result, it is rarely possible to study territorial disputes in captive gibbons, where the only form of non-vocal territorial behaviour is usually directed at substitute territorial rivals such as humans (Orgeldinger, 1997).

Here I describe a particular form of territorial behaviour (i.e., arm-pulling) of siamangs kept in two adjacent cages. I recorded changes in the frequency of this behaviour before and after the formation of a new pair. Because the frequency of territorial disputes in wild gibbons reportedly is "much affected by the number of neighbouring groups, and especially by the appearance of new neighbours" (Gittins and Raemaekers, 1980, p. 75), I expected an increase in inter-group disputes after an adult male was added to the unmated female in one of the cages.

Animals and methods

Observations for this study were carried out as part of a larger project on duet singing and pair bond strength in captive siamang groups (Geissmann, 1986, 1999, 2000).

Fig. 1. The adult siamang pair *Ra* (left) and *Bb* (right) at the Zoo Seeteufel in Studen, Switzerland. Photo: Thomas Geissmann. – *Das erwachsene Siamang-Paar* Ra *(links) und* Bb *(rechts) im Zoo Seeteufel in Studen, Schweiz*.

The study animals were kept in the Zoo Seeteufel in Studen, Switzerland (three groups). The original housing configuration consisted of one solitary adult female *Vr* (Vreneli), one adult pair *Bb*+*Ra* (Bobby and Ratana), and one family group. The male *Bb* of the adult pair *Bb*+*Ra* was wild-born in about 1958 and thought to be infertile. The female of this pair was wild-born in about 1963. This pair has been together since July 1980 (Fig. 1). The solitary female *Vr* was wild-born in about 1963 and remained alone after her offspring and her mate both died in 1979. On 14 July 1981, the adult male *Na* (Narong) was transferred from another zoo to Studen. This resulted in the formation of a new pair *Na*+*Vr*. The arriving male *Na* was wild-born in about 1967 and had produced several offspring with previous mates.

All groups could hear each other during the entire year. During the summer, all three groups were kept in wire-mesh outdoor cages (25 m^2 x 2.5 m) equipped with several horizontal metal bars, ropes, and a wooden sleeping box. Cages one and two stood close together at a sharp angle. The closest distance between the cages (at the corners) was little more than one meter. Here I focus on conflict behaviour observed between the two groups kept in the neighbouring cages one and two.

Agonistic displays directed at the neighbouring group are termed **conflicts** in the following text. During conflicts, rivals often reached out with one arm through the wire mesh towards each other. If they both reached out as far as possible (i.e., up to their shoulders) they were able to grab each other by their hands, whereupon they would begin to pull with considerable force (Fig. 2). I call this behaviour **arm-pulling**.

An additional family group of siamangs was present in Studen but is ignored in the present study. The cage of the family group was located at a distance of more than 10 m from the other two cages. No conflict behaviour was observed in the third group, perhaps because the sight from the third cage to the other two cages was reduced by shrubs and trees.

During the winter, the siamangs were housed in a building. During that season, groups one and two were kept farther apart and no observations on conflict behaviour were possible.

Each conflict bout in groups one and two that included arm-pulling (described below) was counted as one event, independent of its duration or the number of repetitions of arm-pulling. Observations were carried out daily from dawn to dusk, during three blocks of several days each: (1) during the week before the arrival of the new male (7–14 July 1981), (2) during the week after arrival of the new male (15-21 July 1981), and (3) about 2 months after the male's arrival (3–4 Sept. 1981).

All statistical tests (Mann-Whitney *U*; Siegel, 1956) are two-tailed, with a significance level of 0.05.

Fig. 2. Arm-pulling between the adult male siamangs *Na* (left) and *Bb* (right) during a conflict between the pairs *Na*+*Vr* and *Bb*+*Ra*. Note how the wire mesh is deformed by the considerable force applied by the pulling animals. Photos: Thomas Geissmann. – *Armziehen zwischen den erwachsenen Siamang-Männchen* Na *(links) und* Bb *(rechts) während eines Konfliktes zwischen den benachbarten Paaren* Na+Vr *und* Bb+Ra*. Man beachte, wie der Maschendraht durch den Kraftaufwand der ziehenden Tiere nach aussen gedrückt wird.*

Results

Before the arrival of *Na*, conflict behaviour (described below) had been observed only rarely and never reached the intensity level that was later observed. Arm pulling (also described below) was observed only once during the eight days immediately prior to the arrival of *Na* (0.1 events/day), and it occurred between the females *Ra* and *Vr*. In contrast, arm-pulling bouts occurred on average 3.3 times (range 2 – 5) during the eight days immediately after the arrival of *Na*. This difference is statistically significant (Mann-Whitney *U* test, $p < 0.01$). A few small wounds were observed on the palms of *Na*; possibly, the males hurt each other with their fingernails during their arm-pulling behaviour. This did not appear to impede the frequency of arm-pulling. Even two months after the arrival of *Na*, neither conflicts nor arm-pulling (2 events/day) appeared to drop in frequency (Fig. 3).

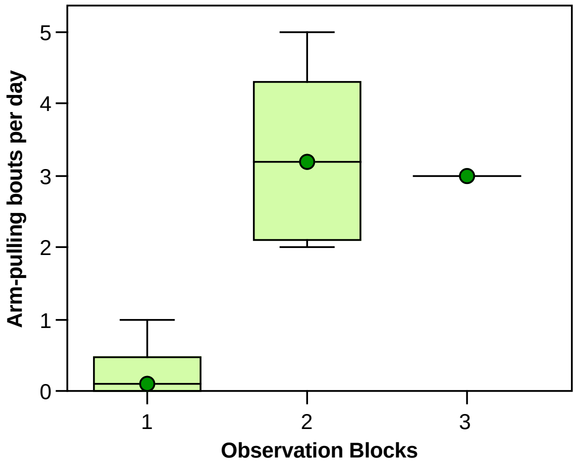

Fig. 3. Arm-pulling bouts per day occurring between two siamang groups. The box plot shows mean, standard deviation, and range of the variable during three observation blocks: (1) during eight days immediately before the arrival of a new male at the zoo; (2) during eight days immediately after pair formation; and (3) during two days about two months after pair formation. – *Häufigkeit des Armziehens pro Tag zwischen zwei Siamanggruppen. Aufgetragen sind Mittelwerte, Standardabweichungen, und Maximum-Minimum-Werte dieser Variablen während drei Beobachtungsblocks: (1) während acht Tagen unmittlebar vor Ankunft des neuen Männchens im Zoo; (2) während acht Tagen unmittlebar nach Bildung des neuen Paares; und (3) während zwei Tagen etwa zwei Monate nach der Paarbildung.*

Several times during each day, the neighbouring pairs *Na*+*Vr* and *Bb*+*Ra* (cages one and two) engaged in mutual agonistic displays. These conflicts consisted of at least one member of each pair going to the corner of the cage where the distance to the opposite cage was shortest. Because there was only one corner in each cage where the opponents were able to touch each other, conflicts always occurred there. Most commonly, all four animals would convene in their respective "conflict corners" at the same time. There, they would sit or hang close to the wire-mesh, facing the other group and intensely staring at their counterparts (similar to the "arched brows" pattern in *Hylobates lar*, Baldwin and Teleki, 1976, p. 33). From time to time, they forcefully threw back their body without letting loose of the wire-mesh, causing considerable noise. When even more aroused, they exhibited a repeated opening and closing of the mouth, all the time staring at the rival. Staring was frequently interrupted by defecating, urinating, and by short bouts of vigorous romping display through the cage, with animals occasionally banging both feet loudly against the wire mesh of the cage walls (*Dreidimensionale Imponierveranstaltung*, Orgeldinger, 1999, p. 75f). *Bb* and *Ra* were occasionally observed biting into the wire mesh. All four animals could simultaneously participate in conflicts, but the brachiation display was more frequently exhibited by the males. Most intimidating displays during conflicts were directed at the neighbour of the same sex (i.e., it occurred after staring at, or after an arm-pulling episode with, that particular animal).

Conflicts usually had a duration of a few minutes and were often accompanied by grunting vocalizations that occasionally developed into song bouts. All song bouts were jointly produced by both groups, and most were initiated by such more or less intense conflicts (Fig. 4). Conflict behaviour was sometimes exhibited during song bouts as well, especially during the "interlude sequences" (Geissmann, 2000). The typical siamang duet song includes a particular phrase ("SFB phrase", Geissmann, 2000) that is usually accompanied by a vigorous brachiation display similar to those occurring during conflicts, but an obvious intrasexual orientation was observed only during the latter.

Fig. 1. The siamang pair *Bb* and *Ra* (behind *Bb*) directs its calling at the neighbouring pair. Photo: Thomas Geissmann. – *Das Siamangpaar* Bb *und* Ra *(teilweise verdeckt) richtet seinen Duettgesang direkt an das Nachbarpaar (nicht im Bild).*

During conflicts, arm-pulling occurred frequently, but typically continued for only a short time (less than one minute). Afterwards, both rivals usually exhibited a short vigorous brachiation display. Arm pulling was observed exclusively between members of the same sex and appeared to occur more frequently among the males. If a female reached her arm out towards the opposite cage, she was virtually ignored by the neighbouring male. On only two occasions were *Vr* and *Bb* observed reaching their arms out towards each other. Both times *Vr* immediately withdrew her arm when the male *Bb* tried to grab her hand, but once he briefly touched her extended hand.

Discussion

The formation of a new pair not only resulted in changes in vocal behaviour (Geissmann, 1986, 1999), but also in other social components such as inter-group agonistic behaviour, as indicated by a significant increase in arm-pulling behaviour. The female *Vr* joined her new mate *Na* frequently and actively participated in inter-group conflicts, whereas she had rarely exhibited this behaviour before *Na*'s arrival. Apparently, she began to behave like a territorial rival and/or was recognized as such as soon as she had a mate.

A similar observation was made in northern Sumatra: "A lone male siamang was tolerated by neighbouring groups until joined by a female; conflicts occurred until the female left" (MacKinnon, cited in Chivers and Raemaekers, 1980, p. 248). In another study on white-handed gibbons (*H. lar*) in peninsular Malaysia, a lone male who frequently produced solo song bouts was tolerated by a family group in the adjacent territory. Only when a lone female began to associate and to produce duet songs with him was he repeatedly attacked by the neighbouring group (MacKinnon and MacKinnon, 1977). These authors suggest that the female song contributions added a special territorial effect to the previously tolerated song of the male.

Field experiments with playbacks of tape-recorded gibbon songs have been conducted on *H. albibarbis*, *H. lar*, and *H. muelleri* but failed to produce consistent differences in the study animals' intensity of response (e.g., orientation, approach, vocalization) to solo songs or duet songs: Responses to female solo songs were at least as intense (Mitani, 1984, 1987) or even more intense (Raemaekers and Raemaekers, 1985) than responses to duet songs, although solo singing is not typical of mated females of any of these species. Only two of the three species responded less frequently to playbacks of males than to those of duet songs (Mitani, 1984, 1987).

It is likely that two gibbons pose a more significant threat than does a solitary individual. Placing an additional siamang in a neighbouring cage, as in the present study, should be expected to elicit an increase in conflict behaviour exhibited by the resident pair, because two neighbours (the new pair) represent twice as large a stimulus as a solitary neighbour. This simple linear model, however, does not suffice to explain the observed increase in arm-pulling behaviour (0.1 events/day *versus* 3.3 events/day) by a factor of roughly 30. Apparently, a siamang pair is more than just the sum of two siamangs.

Arm pulling behaviour occurred exclusively among animals of the same sex, and in the two instances when male and female neighbours reached out toward each other were aborted before any arm-pulling occurred. These observations support the view that territorial behaviour in siamangs and possibly in other gibbons is mostly directed toward animals of the same sex, although active territorial defence is provided predominantly by males in most gibbon species (e.g., Brockelman and Srikosamatara, 1984; Leighton, 1987).

Field experiments on white-handed (*H. lar*) and Mueller's (*H. muelleri*) gibbons also appear to support this view: In both studies, it was the male that more frequently led the group's approach to the loudspeaker when male solo songs were played to the group, and the female when female solo songs were presented (Mitani, 1984; Raemaekers and Raemaekers, 1985). This finding could not be replicated, however, on a third species, the white-bearded gibbon (*H. albibarbis*). There, group approaches were mostly led by males in both situations (Mitani, 1987). The reasons for these contradicting results are unclear. The concept of intra-sexual aggression, although supported by the present study, may be too simplistic to fully explain territorial behaviour in gibbons.

The arm-pulling behaviour observed during my study on captive siamangs is not known of wild siamangs. It may be a substitute of the behaviour normally occurring during inter-group-encounters in wild siamangs, as described by Chivers (1974). The chasing and displays occurring in such situations (see introduction) may allow the neighbours to assess each other's fitness, fighting ability, pair-bond strength and/or determination to defend the territory. These interactions between territory holders appear to be ritualised and only rarely end in fights with physical contact (which would be highly dangerous because the siamangs' long, dagger-like canines make formidable weapons). In the present study, the cages not only prevent the siamangs from chasing each other across the territory boundary but, at the same time, prevent them from leaving that same area. This artificial situation may have provoked the more physical arm-pulling behaviour observed during the present study, and may also be responsible for keeping the number of the territorial interactions at a consistently high level even two months after the initial formation of the new pair.

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Zusammenfassung

Konflikte zwischen zwei Gruppen von Siamangs (*Symphalangus syndactylus*) im Zoo

In der vorliegenden Studie wird das territoriale Verhaltens von Siamangs vor und nach der Bildung eines neuen Paares untersucht. Ursprünglich lebte in einem Käfig ein etabliertes Paar, im benachbarten Käfig ein erwachsenes Weibchen. Nachdem im zweiten Käfig durch Zugabe eines adulten Männchens ein neues Paar gebildet wurde, stieg das territoriale Verhalten zwischen den beiden Gruppen sprunghaft an. Dies äusserte sich unter anderem in einem Anstieg der Duettgesänge beider Gruppen, aber auch in aggressiven Verhaltensweisen zwischen den Gruppen, wie dem “Armziehen”, einer von Gibbons bisher nicht beschriebenen Verhaltensweise. Das Armziehen wurde ausschliesslich zwischen gleichgeschlechtlichen Tieren gezeigt. Der Anstieg des territorialen Verhaltens lässt sich nicht vollständig dadurch erklären, dass ein territoriales Tier mehr vorhanden war, sondern scheint direkt mit der Bildung eines neuen Paares zusammenzuhängen.

Steroid secretion in siamang (*Symphalangus syndactylus*) skin glands

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Chemical composition of secretions of skin glands in hominoid primates have apparently not been analyzed previously, except for the axillary secretions of humans. This paper reports on skin secretions of siamangs (*Symphalangus syndactylus*), a species of gibbons or small apes from Southeast Asia. Secretions were collected and radioimmunoassays (RIA) were carried out in order to check for the presence of the following three steroid hormones: Dehydroepiandrosterone (DHEA), Androstenedione, and Testosterone. This study presents first evidence that high hormone concentrations occurring especially in the sternal area cannot be the result of a simple filtration of hormones out of the blood plasma, but must be the result of a more complex accumulation process. Particularly androstenedione appears to be highly concentrated in the sternal gland. Our findings further support the view that sternal glands in gibbons and axillary glands in humans and African apes may fulfil similar functions, and shed some light on the origin of the axillary organ. We speculate that the accumulation of steroid hormones in siamang skin glands may play a role in olfactory communication.

Introduction

Many primates and other mammals possess specialized glandular concentrations in the sternal area that are commonly used for marking behaviour (Epple, 1986; Geissmann, 1987a). Among hominoids, sternal glands apparently occur only in the gibbons or small apes (Hylobatidae) and orangutans (genus *Pongo*) of Southeast Asia (Brandes, 1939; Geissmann, 1986, 1987a; Geissmann and Hulftegger, 1994; Schultz, 1921; Wislocki and Schultz, 1925). In orangutans and one gibbon species, the siamang (*Symphalangus syndactylus*), sternal gland secretions exhibit a strong, genus-specific odour (Geissmann, 1987a and unpublished observations), as do axillary gland secretions in gorillas and humans. In Asian apes, sternal glands apparently are not used for any kind of marking behaviour (Geissmann, 1986, 1987a; Geissmann and Hulftegger, 1994), and this generally appears to apply to axillary glands in African apes and humans, as well. The sternal glands of gibbons show similarities to the axillary glands of humans and the African apes in both the macroscopic aspect of the glands and their microscopic structure (Geissmann and Hulftegger, 1994). In addition, secretory activity of both types of glands appears to increase in similar situations: during stress and in response to elevated temperature (Geissmann, 1986, 1987a, b; Geissmann and Hulftegger, 1994). In some gibbons (individuals of several species), concentrations of coloured pores can be found in the axillary region. Dried glandular secretion of red-brown colouration can be seen in the skin pores or near the hair roots. These fields are usually connected with the sternal glands (Geissmann and Hulftegger, 1994).

The human axillary gland is generally believed to play a role in olfactory communication (Hold and Schleidt, 1977; Labows, *et al.*, 1982; Russell, 1976; Schleidt and Hold, 1982a, b; Stoddart, 1990). The functions of the sternal glands in Asian apes, on the other hand, are completely unknown.

Chemical compositions of these glandular secretions have apparently not been analyzed previously, except for the axillary secretions of humans. The axillary area is probably the most conspicuous scent-producing specialization of the human skin and the only one generally recognized as a “scent organ” by dermatologists, zoologists, and chemists (Schaal and Porter, 1991). Axillary secretions contain lipids (mainly fatty acids and steroids) and approximately 10% protein (including a number of enzymes) (e.g. Gower and Ruparelia, 1993; Gower, *et al.*, 1985, 1988; Labows, *et al.*, 1982; Labows, 1988).

Much of the musk-like or urine-like smell that is reported from the human axilla (see for example review in Stoddart, 1990) is caused by at least two odorous Δ^{16}-androgen steroids: 3α-androstenol (5α-androst-16-en-3α-ol) and 5α-androstenone (5α-androst-16-en-3-one) (Brooksbank, *et al.*, 1974; Claus and Alsing, 1976; Gower, *et al.*, 1985). The former, an alcohol, has a musky odour and “is not altogether unpleasant”, whereas the latter, a ketone, confers the disagreeable and dominant odour that has been characterized as “urine”, “sweaty” and “perspiration” in odour description studies (Labows *et al*., 1982, p. 199f). Studies utilizing radioimmunoassay techniques have demonstrated significant differences in concentration of 5α-androstenone in men and women (Bird and Gower, 1981; Gower *et al*., 1985).

Freshly-secreted apocrine sweat is odourless (Hurley and Shelley, 1960; Shelley *et al*., 1953); it contains little or no 3α-androstenol or 5α-androstenone, but cholesterol, dehydroepiandrosterone sulfate, and androsterone sulfate (Labows *et al*., 1979). Although the two sulfated steroids are closely related to the odorous steroids in their chemical structure, it is unknown whether either of these is a precursor of the latter (Gower and Ruparelia, 1993; Labows *et al*., 1982).

Because of the numerous similarities between sternal and axillary glands mentioned above, and because gibbons are relatively closely related to humans (Geissmann, 1995b, 2003), it has previously been suggested that both glands also share similarities in their functions (Geissmann, 1987a; Geissmann and Hulftegger, 1994). If this were the case, we should expect that gibbon sternal glands, like human axillary glands, produce steroid hormones and their derivates. In order to test this hypothesis, we collected skin secretions of several siamangs (*S. syndactylus*) and checked for the presence of steroid hormones by radioimmunoassays (RIA).

Radioimmunoassays of steroid hormones are routinely carried out on human urine samples at the Kinderspital of Zürich. The following three hormones have been analyzed for this study because their antisera were easily available, and because of their supposed function in olfactory communication in humans and pigs (e.g. Claus and Alsing, 1976): dehydroepiandrosterone (DHEA; 3β-hydroxy-androst-5-en-17-one), androstenedione (4-androstene-3,17-dione), and testosterone (17β-hydroxy-androst-4-en-3-one).

Materials and methods

The following age classes for captive gibbons were recognized in this study: infants 0-2 years of age; juveniles 2.1-4 years; subadults 4.1-6 years; adults more than 6 years, as proposed by Geissmann (1995a).

Between July 1986 and January 1991, a total of 36 samples (including 6 control blanks which will be described below) were collected for analysis using a radioimmunoassay technique. All samples of skin secretions were collected by one of us (T.G.). Most of them were collected from anaesthetized animals, the other stem from tame animals or from zoo animals that died less than 24 hours before examination. It is important to note that the study animals were not sedated for the purpose of this investigation, but for management reasons (e.g. for veterinary checks, veterinary treatment, or transport). Several zoos were asked to indicate when such intervention was scheduled, and visits were timed accordingly.

The study animals were kept at the Zoo Hellabrunn in Munich (Germany) and at Zürich Zoo (Switzerland). Two individuals were examined twice at an interval of 0.9 and 2.6 years, respectively. The data from such repeated examinations were analyzed separately. Table 1 lists the number of samples collected at the two institutions. For most animals, secretion samples were collected in the sternal and axillary areas, but for some individuals additional samples were taken from other body parts (Fig. 1). One sample was collected in the circumgenital area. This area is not labelled in the figure, because it was pooled with the samples of the inguinal area in order to increase the sample size for each area. All samples labelled as “dorsal” refer to the area between the shoulder blades in the midsagittal plane.

Table 1. Number of samples of skin secretions collected for this study. The numbers in brackets represent the numbers of individuals. – *Anzahl und Herkunft der Proben von Hautdrüdsensekreten. Zahlen in Klammern bezeichnen die Anzahl der untersuchten Individuen*.

Samples	Munich Zoo	Zürich Zoo	Total
Adults and subadults	9 (2)	14 (3) [a]	23 (5)
Juveniles and infants	–	7 (3)	7 (3)
Control blanks	–	6	6
Total	9 (2)	27 (6)	36 (8)

(a) Includes 3 plasma samples

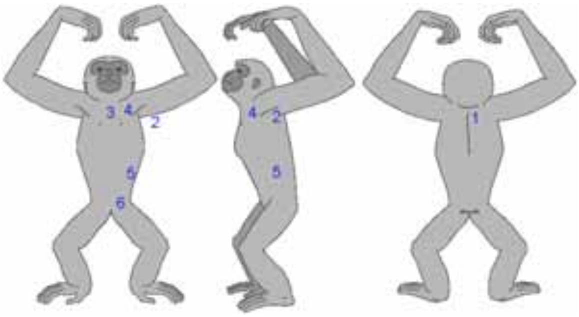

Fig. 1. Sites from which secretion samples were taken: (1) dorsal (interscapular); (2) axillary; (3) sternal; (4) lateral chest (claviculary); (5) lateral abdominal; (6) inguinal. – *Körperstellen, an welchen Hautdrüsensekrete gesammelt wurden: (1) Rücken (interscapular); (2) axillar; (3) sternal; (4) seitliche Brust (clavicular); (5) seitlicher Rumpf; (6) inguinal.*

Unless otherwise stated, samples were collected in a standardized way: After the animal was sedated, sterile compresses (TELFA, Kendall Company Boston, USA) were moistened with pure ethanol (per analysis, 99%) and rubbed with slight pressure 12 times over a selected spot of the animal’s skin. In order to avoid contamination of the samples with human steroid hormones, a fresh pair of medical gloves was used for the collection of each sample.

Six control samples of various hormone concentrations (Table 2), types and sampling procedures were used. Three unmanipulated TELFA compresses were used as control samples (Nos. 1-3, Table 2). The highest steroid concentrations found by RIA in any of the three control samples were then subtracted from the hormone values of most secretion samples (exceptions described below) to eliminate the "background noise" due to the sensitivity of the RIA technique. This procedure will be referred to as "standard correction" in the following text.

Table 2. Hormone concentrations used as controls (ng/sample).[1] – *Hormonkonzentrationen der Kontrollstichproben (ng/Stichprobe).*

Control sample No.	DHEA[2]	Androstene dione	Testo-sterone
1	0.8	0.7	0.8
2	1.1	0.6	0.4
3	0.8	0.8	0.4
4	–0.9	8.3	–3.0
5	0.7	3.0	2.2
6	0.0	0.3	0.0

(1) See text for a description of the different types of controls and explanation for negative values in control No. 4.

(2) DHEA = Dehydroepiandrosterone

In the following cases, special corrections were necessary: In a few instances, an opportunity for collecting secretion samples arose when no gloves where available. Although the author then washed his hands with great care before collecting every single sample, the TELFA compresses possibly became contaminated to some degree with human steroid hormones during the rubbing procedure. In order to measure the amount of possible contamination, two samples were collected from adjacent areas on the back of the same animal; one sample was collected with gloves, the other one without gloves. The difference in the hormone concentrations between the two samples is shown in Table 2 as control No. 4. In two hormone concentrations (DHEA and Testosterone), the value for the sample collected without gloves was lower than the value for the sample collected with gloves (resulting in negative values in Table 2), which is the opposite of what should be expected if the samples had been contaminated by the investigator. The sample collected without gloves had considerably higher concentrations only for androstenedione, probably as a result of contamination. This possible amount of androstenedione contamination was subtracted from all samples that had been collected without gloves.

In another control test, the author intensively manipulated one new TELFA compress with ethanol. The androstenedione and testosterone (but not the DHEA) levels measured on this control sample (No. 5, Table 2) are slightly higher than the "standard corrections" described above. The difference may be due to contamination. The testosterone concentration found in this control sample has accordingly been subtracted from all samples collected without gloves. For androstenedione, the higher correction value described above (control No. 5) has been used for samples collected without gloves. For DHEA, the "standard correction" measured on control sample 2 was the highest correction value found; therefore, it was also used for the samples collected without gloves.

A small amount of pure exudate from the sternal gland was collected in a test tube directly from the fur of a study animal. In this case, an empty test tube served as a control sample (control No. 6, Table 2).

Because the exact amount of secretion collected with the rubbing method could not be determined, hormone concentrations are given in ng per compress, unless stated otherwise.

A case of unusually profuse sternal secretion was once observed in the adult male siamang "Bohorok", which had been hand-reared at the Zürich Zoo, and was more than 11 years old in October 1986, when the following observation was made in front of the outdoor cage. The male was observed to exhibit both sudden agitation and a discharge of sternal exudate, probably caused by the sight of its former caretaker (U. Rathfelder) carrying an infant siamang (which also had to be hand-reared). The adult male alternatingly bit into the wire-mesh of his cage and stared at Mrs. Rathfelder, who was standing a few meters away from the cage talking to other staff members. The typical odour of the siamang became very strong, and sternal secretion could actually be seen trickling down from the male's sternal gland. This was the only situation in which pure, fresh secretion from the sternal gland of a gibbon was collected during this study.

All Radioimmunoassays (RIA) were carried out at the Kinderspital Zürich, using antisera purchased from bioMérieux. After adding tracer amounts of [3H]dehydroepiandrosterone (DHEA), [3H]androstenedione, or [3H]testosterone to monitor recovery, samples were extracted by methylene chloride extraction. All immunoassays used the dextran-coated charcoal separation method.

Pearson correlations between age and hormone concentrations were calculated using StatView version 5.0.1 (SAS Inst.) on an Apple PowerBook G4 computer. The occurrence of a linear relationship between the dependent variables (hormone concentrations) and the independent variable (age) was tested with a *t*-test, and the occurrence of a correlation between the variables was tested with a *z*-test.

Results

Table 3 lists the hormone concentrations measured in each sample. Table 4 presents summary statistics of the hormone concentrations in the sternal region and the axillary region, respectively, for adult animals (and one subadult) of each sex separately. Within most hormone sex classes, considerable variation in the hormone concentrations is apparent from comparison of the minimum and maximum values. Although the samples are too small to permit a statistical test for sex differences, the values in Table 4 at least suggest such differences in some cases: Both sternal and axillary DHEA appear to be higher in females than in males.

The findings in Table 4 refer only to secretions collected in the sternal and the axillary areas. In several individuals, a few secretion samples were also collected in other areas of the skin. Figure 2 shows the average hormone concentrations of adult and subadult females and males in all the six sampled skin areas. By far the highest concentrations are found in the sternal area.

Figure 3 shows hormone concentrations in the sternal and axillary area plotted against age of the study animals. For this figure, all adult animals (i.e. animals older than 6 years) were pooled. All plots show a positive correlation between hormone concentration and the age of the siamangs, with one exception: axillary DHEA has a negative correlation with the age of the study animals. Of these correlations, however, only one is statistically significant: Sternal androstenedione concentration exhibits a linear relationship with age (*t*-test, $p<0.05$) and is positively correlated with age ($r=0.71$, $n=8$; *z*-test, $p<0.05$). All other correlations are not significant ($p>0.05$), although the correlation between sternal testosterone and age is close to significance (*t*-test, $p<0.06$; $r=0.69$, $n=8$; *z*-test, $p<0.06$).

Table 3. Hormone concentrations in siamang samples.(1) – *Hormonkonzentrationen in den Siamang-Stichproben*.

Age, Sex	**Sample Type**	**DHEA**	**Andro-stene-dione**	**Testo-sterone**
ad. M ("Bo-horok")	pure exudate	5.2	143.2	2.2
	sternal	20.1	255.2	15.0
	axillary	7.1	14.9	2.2
	inguinal	3.8	23.8	6.6
	dorsal	4.3	7.6	1.4
	plasma	(694)	(635)	(992)
ad. F	sternal	31.8	0	2.7
	axillary	28.2	0	0.4
	plasma	(280)	(238)	(82)
ad. F	sternal	23.8	205.2	12.7
	axillary	6.2	11.8	2.7
	inguinal	3.0	7.8	3.2
	dorsal	3.7	5.0	2.0
	plasma	(481)	(288)	(144)
ad. F	sternal	22.2	327.7	10.5
	axillary	8.1	11.4	0.6
	inguinal	13.4	19.4	7.3
	lat. abdomen	9.2	12.9	4.8
sad. M, 4.52 years	sternal	22.6	67.6	10.5
	clavicular	10.3	6.6	4.1
	axillary	8.0	10.2	0.7
	circumgenital	11.8	8.0	4.4
	lat. abdomen	11.0	5.6	4.0
juv. M, 2.27 years	sternal	9.3	12.59	1.1
	axillary	13.8	19.2	0.5
	inguinal	12.8	8.6	5.1
	dorsal	11.6	8.4	4.2
inf. M, 1.51 years	sternal	34.6	1.3	0.6
	axillary	29.7	0	0.4
inf. M, 0.64 years	sternal	11.3	0	0.8

(1) All hormone concentrations were corrected as described above (Animals and Methods section). Hormone concentrations were measured in ng/sample, except plasma samples (values in brackets), which are presented as ng/dl. Abbreviations: ad. = adult; sad. = subadult; juv. = juvenile; inf. = infant; M = male; F = female; lat. = lateral.

Table 4. Means of hormone concentrations in the sternal and axillary samples (ng/sample) of male and female animals.(1) – *Mittelwerte der Hormonkonzentrationen in den Stichproben der Sternal- und Axillar-Region von männlichen und weiblichen Siamangs*.

Samples	**Males**					**Females**				
	N	Mean	SE	Min.	Max.	N	Mean	SE	Min.	Max.
Sternal:										
DHEA	2	21.4	1.3	20.1	22.6	3	25.9	3.0	22.2	31.8
Androstenedione	2	161.4	93.8	67.6	255.2	3	177.6	95.6	0	327.7
Testosterone	2	12.7	2.3	10.5	15.0	3	14.8	7.7	2.7	29.1
Axillary:										
DHEA	2	7.6	0.5	7.1	8.0	3	14.2	7.1	6.2	28.2
Androstenedione	2	12.5	2.4	10.2	14.9	3	7.7	3.9	0	11.8
Testosterone	2	1.4	0.7	0.7	2.2	3	1.2	0.7	0.4	2.6

(1) Abbreviations: N = number or individuals; SE = standard error.

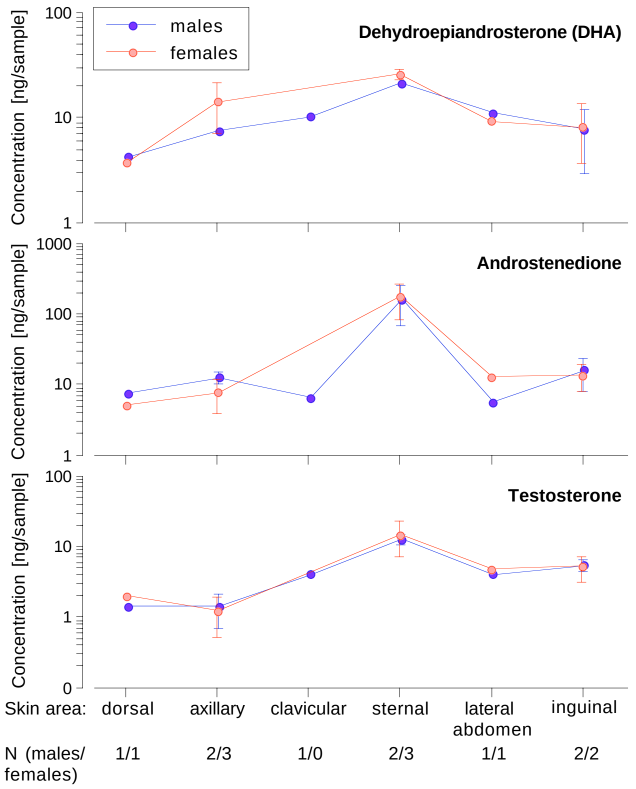

Fig. 2. Average concentrations of three steroid hormones in six skin areas of male and female siamangs. Error bars are standard errors. – *Mittelwerte (und Standardfehler) der Hormonkonzentrationen in den Stichproben von sechs verschiedenen Hautregionen von männlichen und weiblichen Siamangs. Die unterste Zeile gibt die Stichprobengrösse an (Männchen/Weibchen).*

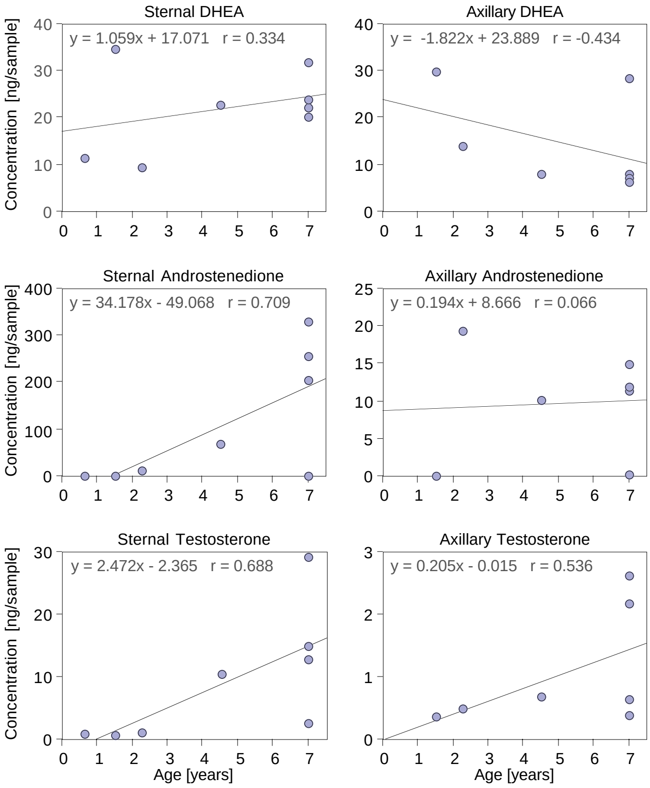

Fig. 3. Concentrations of three steroid hormones in the sternal and axillary areas plotted against age of the study animals. Adult siamangs (i.e. animals older than 6 years) are pooled. – *Konzentrationen von drei Steroidhormonen in den sternalen und axillaren Hautregionen, aufgetragen gegen das Alter der untersuchten Siamangs. Erwachsene Tiere (d.h. Tiere, die älter als sechs Jahre waren) wurden zusammengefasst.*

Of particular importance for the interpretation are the hormone concentrations determined for the sample of pure sternal secretion of the adult male siamang “Bohorok”.

One to three droplets of pure exudate were collected through the wire-mesh directly from the tame animal’s fur with a piece of fresh paper nappy. The hormone concentrations determined from this sample are shown in Table 5 (line 1). Although the exact amount of secretion is not known, the quantity of one to three droplets was determined to correspond to $2 \cdot 10^{-4}$ – $9 \cdot 10^{-4}$ dl. This range is a maximum estimate obtained by repeatedly measuring drops of water that were large enough to fall down from a syringe opening of 1 mm in width. The collected exudate droplets of the male siamang were, if anything, smaller than that. With the above estimate of exudate quantity, the hormone concentrations in the exudate can be calculated (Table 5, line 2). These are conservative values, because the quantity of exudate may be smaller (but certainly not larger) than assumed here.

For comparison, three samples of siamang blood plasma were collected. One of the samples stems from the same male as the pure sternal secretion. The hormone concentrations in the plasma samples show some variation (Table 5, line 3), but even the highest concentrations in the plasma samples are several times lower than the most conservative concentration estimate of the sternal sample. The difference amounts to a factor of at least 2.4 for testosterone, but up to 250 for androstenedione (Table 5, line 4).

On the other hand, the hormone concentrations in the siamang plasma samples are roughly similar to those of humans (adapted from Labhart *et al*., 1986, p. 523), except for the relatively high concentrations of androstenedione in the siamangs (Table 5, line 5).

Table 5. Determination of hormone concentration in the sternal secretion in an adult male siamang (“Bohorok”). – *Bestimmung der Hormonkonzentration im Sternalsekret des erwachsenen Siamang-Männchens “Bohorok”.*

			DHEA	Androstenedione	Testosterone
1.	Concentration in secretion sample (ng / sample), ad. siamang male “Bohorok”		5.2	143.2	2.2
2.	Concentration in secretion sample (ng / dl), estimate,	Maximum	26 000	716 000	11 000
	ad. siamang male “Bohorok”	Minimum	5 800	159 100	2 400
3.	Concentration in peripheral plasma (ng / dl):				
	ad. siamang female “Gaspa”	22 Jan. 1987	280	238	82
	ad. siamang female “Gaspa”	30 Aug. 1989	481	288	144
	ad. siamang male “Bohorok”	30 Aug. 1989	694	635	992
4.	Accumulation factor,				
	ad. siamang male “Bohorok”	Minimum	8.4	250.6	2.4
5.	Concentration in peripheral plasma (ng / dl) (Labhart *et al*., 1986, p. 523)				
	Men (20-40 years)		130-1270	60-230	300-1300
	Women (20-40 years)		140-1250	50-330	4-70

Discussion

Chemical analysis of the secretion of specialized skin glands has been carried out on only a few primate species. Apart from studies on humans, steroids have been found as a major component of glandular secretion only in exudates from the brachial glands of *Nycticebus* (Alterman, 1989). It is possible, however, that steroids have simply not been examined in previous studies. Certain steroid hormones produced in the axilla are thought to be of major importance in human olfactory communication. The present study shows that steroid hormones are accumulated in the skin glands of at least one gibbon species, the siamang (*S. syndactylus*). This steroid secretion is not sex-specific. It is most pronounced in the sternal gland and, to a lesser extent, in the axillary region. Secretory activity may not be fully developed in immature siamangs.

The samples we collected consisted primarily of dried secretion rubbed from the skin with ethanol-soaked compresses. Although the hormone concentrations of these samples can be compared with each other, they give no information on the hormone concentration in the pure fresh secretion. Such information, albeit as a rough approximation, was derived from our single sample of pure sternal exudate collected from the adult male siamang “Bohorok”. Hormone concentrations in this exudate are several times higher than the concentrations found in the peripheral plasma of the same siamang. This finding is of importance for determining the mechanism of how the hormones are secretioned in the sternal gland of siamangs: The high sternal hormone concentrations cannot be the result of a simple filtration of hormones out of the blood plasma, but must be the result of a more complex accumulation process. This accumulation is by a factor of at least 2.4 and 8.4 in testosterone and DHEA, respectively (conservative estimates), but by a factor of at least 250 in androstenedione in the male siamang studied here.

Because skin secretions have been collected in a standardized way, they can be compared with the sternal sample of the adult male “Bohorok”, with the latter serving as a standard. All relative hormone concentrations that are as high or even higher than those of the standard (i.e. “Bohorok”) probably result from an accumulation process as well. In addition, they suggest the presence of actively secreting glandular fields.

Especially high hormone concentrations (higher than those of “Bohorok”) are found in the sternal samples of three adult females, one subadult male and one infant male (see Table 3). Hormone concentrations surpassing those of “Bohorok” are almost completely restricted to DHEA (only one adult female also had higher androstenedione concentrations). In at least two of these animals, DHEA accumulation apparently occurs in the axillary region as well (1 adult female and 1 infant male).

Because the system of skin glands in gibbons and the axillary glands of humans and the African apes share numerous similarities, it has previously been speculated that they may also serve related functions (Geissmann, 1987a; Geissmann and Hulftegger, 1994). Our study presents first evidence that steroid hormones are accumulated in siamang sternal and (to a lesser extent) axillary glands. Although the functions of this steroid accumulation remain speculative, our results fully support our initial hypothesis, thus providing further support to the view that siamang sternal glands and human axillary glands may exhibit similar functions, including a role in olfactory communication.

It is unlikely that all the similarities between the system of skin glands in gibbons and the axillary glands of humans and the African apes evolved independently in the two clades. It has not previously been possible to explain the phylogenetic origin of the axillary glands. The results presented in this study suggest that axillary glands and sternal glands may have both evolved from the same phylogenetic precursor. Secretion of steroid hormones probably already occurred in the common ancestor of gibbons, the great apes and humans (i.e., the Hominoidea).

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Zusammenfassung

Steroid-Ausscheidung durch Hautdrüsen beim Siamang (*Symphalangus syndactylus*)

Über die chemische Zusammensetzung von Hautdrüsensekreten bei Menschenaffen liegen bisher anscheinend keine Studien vor. In der vorliegenden Arbeit wurden Hautsekrete des Siamangs (*Symphalangus syndactylus*), des grössten Vertreters der südostasiatischen Gibbons oder kleinen Menschenaffen, untersucht. Sekrete von Individuen verschiedener Altersklassen und beider Geschlechter wurden gesammelt und mit Hilfe von Radioimmunoassays (RIA) auf das Vorhandensein der folgenden drei Steroidhormone überprüft: Dehydroepiandrosteron (DHEA), Androstenedion, und Testosteron. Die Resultate zeigen, dass vor allem in der Sternalregion hohe Hormonkonzentrationen auftreten. Diese können nicht die Folge einfacher Filtration aus dem Blutplasma sein, sondern müssen durch einen komplexeren Anreicherungsprozess zustande gekommen sein. Unsere Studie erbringt zudem erste Hinweise darauf, dass die Sternaldrüsen der Gibbons und die Achselhöhlendrüsen der afrikanischen Menschenaffen und des Menschen ähnliche Funktionen erfüllen könnten. Dies wirft möglicherweise auch ein erstes Licht auf den evolutiven Ursprung der Achselhöhlendrüsen. Es wird vermutet, dass die Anreicherung von Steroidhormonen in bestimmen Hautdrüsenregionen der Siamangs eine Rolle in der olfaktorischen Kommunikation spielen könnte.

A primate “motor theory of sound perception”: Three case studies with gibbons

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The “motor theory of speech perception” by Liberman *et al.* (1967) is a popular neurolinguistic theory that attempts to explain how speech sounds (phonemes) are perceived by the human brain. It has been shown that one and the same phoneme can have different acoustic realizations, depending on the sound context it is embedded in. The phoneme /g/ has different acoustic characteristics in the words “geese” and “goose” since it anticipates features of the following [i] and [u] sounds, respectively. This process of assimilating adjacent speech sounds is known as *co-articulation*, and it leads to changes in the acoustic nature of sounds. Therefore, when co-articulation occurs, acoustic description cannot solely define a phoneme. The “motor theory” proposes that the articulatory gesture (vocal tract gesture) that underlies every speech sound is the actual percept of speech since it is of invariant and stable nature. In this paper, song vocalizations of three gibbons (including the species *Nomascus leucogenys, Hylobates muelleri*, and *H. agilis*) are analyzed. The results provide first indications that co-articulation occurs in the calls of each species. This suggests that the acoustic signal itself is unstable and does not function as the only determinant of sounds. If this is correct, gibbons – in a way similar to humans – may perceive sounds according to their articulatory gestures rather than solely their acoustic features.

Introduction

The motor theory of speech perception

The “motor theory of speech perception” was developed in the 1960’s by Alvin Liberman and colleagues at the Haskins Laboratories. Although speech sounds are strictly defined by their formant frequency structure, it is possible that a sound can have various acoustic realities. Formant frequencies (or formants) are concentrations of acoustic energy around certain frequencies in sound waves of the vocal tract. They become visible as dark bands on sonagrams; the lowest formant is called the “fundamental frequency” (or F0), the higher formants are labelled ‘first formant’ or F1, ‘second formant’ or F2, and so forth. Every speech sound has a characteristic formant structure that determines its quality.

Liberman *et al.* (1954) found that the transition of F2 (upward or downward movement of the second formant) can be different in consonants, depending on the vocalic environment (Fig. 1). F2 transition in [di] is high and rising (according to the high second formant for [i]), while F2 transition in [du] is low and falling (according to the lower second formant for [u]).

The speech sound /d/ is produced by forming a constriction of the tongue tip against the alveolar ridge of the hard palate; this constriction is altered by the articulation place of the succeeding vowel. Since there are two acoustically different realizations of /d/ in the syllables [di] and [du], the acoustic features cannot be the sole determinant of this speech sound. Liberman *et al.* concluded that it must be the articulatory gesture (e.g. forming the tongue constriction) that determines the speech sound.

These findings led Liberman and colleagues to assume that one consonant can have different acoustic patterns but only one articulatory gesture. Liberman *et al.* (1967) proposed that speech perception cannot solely rely on acoustic features but that the acoustic features function as indicators for the underlying, real percept of speech sounds, which is the motor gesture of the articulatory organs (Liberman and Mattingly, 1985).

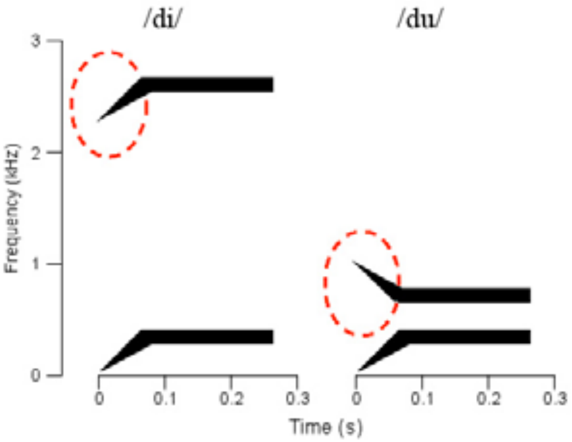

Fig. 1. Second formant transitions (after Galantucci *et al.* 2006). – Unterschiedliche *Transition der zweiten Formanten (F2) des Konsonanten [d] in Abhängigkeit des nachfolgenden Vokals [i] oder [u] (nach Galantucci et al., 2006).*

Liberman and colleagues discovered that, due to the motoric nature of speech sounds, segments are co-articulated during speech. Co-articulation describes the process when vocal gestures for successive consonants and vowels, e.g. tongue or lip positions, overlap in time (Fig. 2). This led to the proposal by Liberman *et al.* (1967) that speech is not an acoustic "alphabet", with phonemes articulated chronologically, but that speech is an "efficient code", with individual segments assimilating to one another, depending on the sound environment.

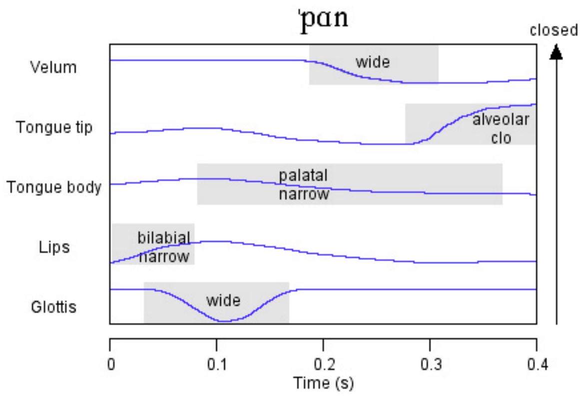

Fig. 2. Gestural score for the English word "pan" (after Goldstein and Fowler, 2003, and Haskins Laboratories, 2008). – *Gesturaler Ablaufplan für das englische Wort «pan» (nach Goldstein und Fowler, 2003*, und Haskins Laboratories, 2008*).*

Liberman *et al.* (1967) state that the new phylogenetic adaptations that are unique to the human species include the skills (1) to co-articulate speech and (2) to perceive co-articulated speech. Since one of them by itself cannot be useful, both were suggested to have co-evolved.

Doherty *et al.* (1983) provide evidence to support the theory that perception and production systems are genetically coupled. They cite evidence from frog hybrid species where females react preferably to male mate calls of the same breed of hybrids and show significantly less reaction to mate calls from other hybrids or the original breeds. The authors state that since communicative parity must be preserved to enable inter-individual communication systems, the perception and production mechanisms must be linked genetically. However, Jarvis and Nottebohm (1997) provide a different interpretation for the hybrid call preferences. They suggest that co-evolutionary processes relying on genetic correlations rather than on genetic coupling equip species with a preference for calls of conspecifics of the same breed.

Extending the theory to bird songs

Based on the 'motor theory of speech perception', Williams and Nottebohm (1985) conducted experiments with song birds (oscines) to find out whether they perceive sound units as sequences of vocal tract gestures. They made recordings in the higher vocal centre and the trachiosyringeal portion of the hypoglossal nerve (nXIIts) of male zebra finches and found evidence that birds perceive sounds as a series of articulatory gestures. The motor neurons in nXIIts of the zebra finches were shown to react differently to different types of syllables in the songs. Frequency modulated signals resulted in excitation of neurons located in the posterior portion of nXIIts, whereas unmodulated high frequency signals had an inhibitory effect. Frequency-modulated syllables were shown to have an inhibitory effect in the anterior portion of the nXIIts, where unmodulated high-frequency syllables had an excitatory effect (for review see Hauser, 1996, p. 148). The authors conclude that the birds can only perceive acoustic features of syllables through conversion of the acoustic percept into a series of motor actions. The same motor actions are required to produce and to perceive particular song units.

Similar to what Liberman and Mattingly (1985) argue for humans, the avian neural pathways for song perception and song production are suggested to be intimately connected (Williams and Nottebohm, 1985).

Co-articulation

Liberman *et al.* (1967) define 'co-articulation' as a uniquely human mechanism of overlapping articulatory gestures. Due to the rapid sequencing of motor gestures of the articulating organs, transitions between the gestures are blurred and the gestures start to assimilate partially, causing 'co-articulation'. 'Co-articulation' becomes visible on sonagrams when sounds are articulated while still features of the preceding or succeeding sounds are retained (Fig. 3).

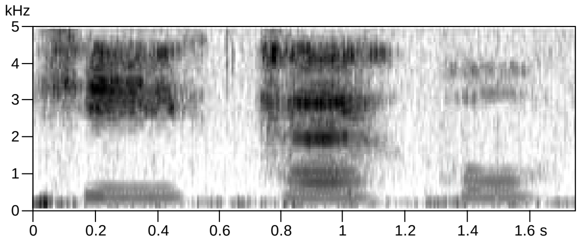

Fig. 3. [hi-hɛ-ho] of female German speaker. Note the co-articulated allophones of /h/. The sonagram plots time on the x-axis and frequency on the y-axis. – *[hi-hɛ-ho] einer deutschen Frauenstimme. Die koartikulierten Allophone von /h/ sind gut sichtbar. Das Sonagramm verzeichnet Zeit (t) auf der x-Achse und Frequenz auf der y-Achse*

The sonagrams show that the /h/ has a different onset with each vowel, i.e. the allophones of /h/ show different frequency ranges due to influence from the succeeding vowels. The different frequency ranges are evidence for differences in articulation of the allophones.

Vowels that require a high tongue position produce higher formants; when the consonant /h/ – in anticipation of the pronunciation of [i] – is produced with the tongue already in position for [i], the overtone structure of /h/ will start to resemble the frequency patterns of the vowel.

Analyses of the envelopes reveal different curve structures for each one of the co-articulated /h/ sounds (Fig. 4).

It becomes evident that the front high vowel (in Fig. 4a) causes the harmonics of /h/ to be higher, while the back close vowel (Fig. 4c) causes /h/ to assimilate the harmonics to the lower frequencies. This process is known as co-articulation.

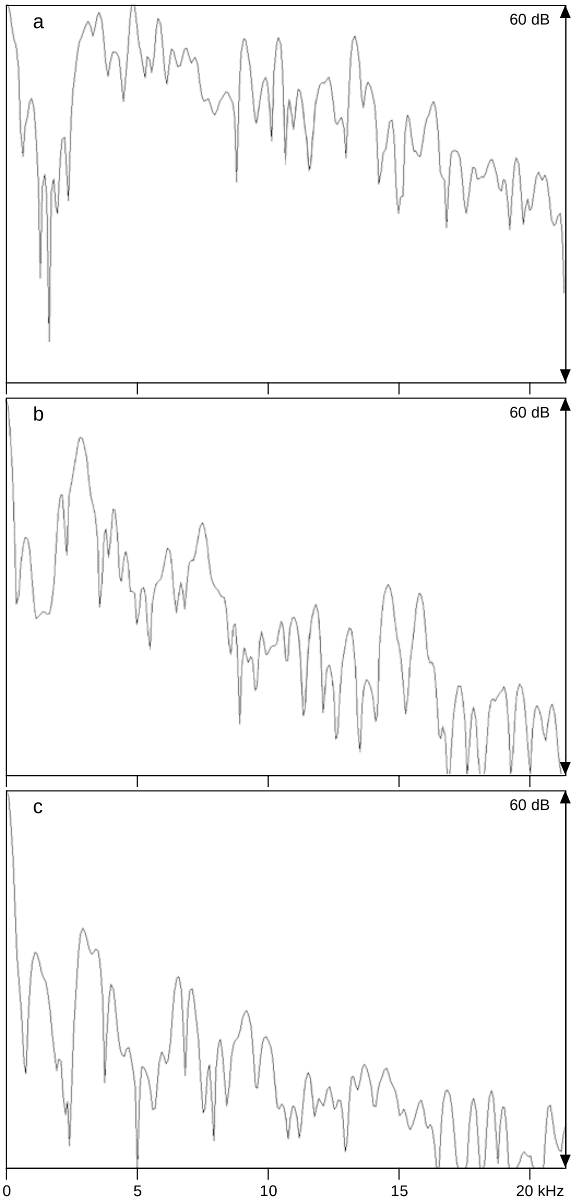

Fig. 4. Spectral slices (sound intensity vs. sound frequency, according to Fourier transformation) of allophones of /h/ in [hi] (a), [hɛ] (b), and [ho] (c). – *Spektraler Ausschnitt (Intensität vs. Frequenz, nach Fourier transformiert) der Allophone von /h/ in [hi] (a), [hɛ] (b), and [ho] (c).*

Goal of this study

Song vocalizations of three gibbons were analysed to look for 'co-articulation' effects.

Naturally it would be predicted that mouth articulation gestures overlap during rapid production of sound sequences. Such a process would indicate that the acoustic properties of the individual sound segments themselves do not convey meaning, as they can be differently realized depending on the sound environment. In that case, sound perception could be the identification of the motor gesture that underlies the acoustic signal, in analogy to the mechanism proposed by Liberman *et al.* (1967) for sound perception in humans.

Material and Methods

The acoustic analyses were conducted on one sound sample each of (1) a male northern white-cheeked crested gibbon (*Nomascus leucogenys*) (duration: 15 seconds, sampling rate: 44,100 kHz), (2) a male Bornean or Müller's gibbon (*Hylobates muelleri*) (duration: 70 seconds, sampling rate: 44,100 kHz) and (3) a female agile gibbon (*H. agilis*) (duration: 20 seconds, sampling rate: 44,100 kHz).

Audio material was kindly provided by Thomas Geissmann, University Zürich-Irchel, who made the recordings of the two male animals: Sample 1 is part of a duet song bout of *N. leucogenys* tape-recorded at the Ménagerie du Jardin des Plantes, Paris (France) on May 17, 1988; Sample 2 is part of a male solo song bout of *H. muelleri* tape-recorded on May 27, 1988, at the Zoo Doué-la-Fontaine (France). Sample 3 of a female *H. agilis* was recorded by Charles Welch at the Louisiana Purchase Garden in Monroe (USA) in September 1979. The recording was provided by Thomas Geissmann.

The acoustic analyses of this paper were conducted with the speech analysis software "Praat 5.0.11", developed by the University of Amsterdam (Boersma and Weenink, 2008), and the audio program "Soundstudio 3.5." for MacOSX 10.4 (Kwok, 2007).

The organisation of song bouts in crested gibbons (genus *Nomascus*) has been described in several studies (Deputte, 1982; Geissmann *et al.*, 2000; Haimoff, 1984b; Konrad and Geissmann, 2006; Schilling, 1984). Fully developed song phrases of adult male crested gibbons typically consist of three different note types (Fig. 5a): (1) The boom notes (alternatively termed *ma* notes) are very deep notes of constant frequency and are produced during inflation of the throat sac. Crested gibbon males usually produce boom notes as single notes instead of short series or phrases typical of other male notes. (2) The *aa* notes (*mb* notes) are short, relatively monotonally repeated sounds, also referred to as staccato notes. (3) The most conspicuous part of the male song is the multi-modulated phrase (*mc* notes), consisting of several notes that exhibit rapid and steep frequency modulations. In a fully developed male song bout, the male singer typically cycles through the three types of phrases (boom, staccato, and multi-modulated – usually in this order).

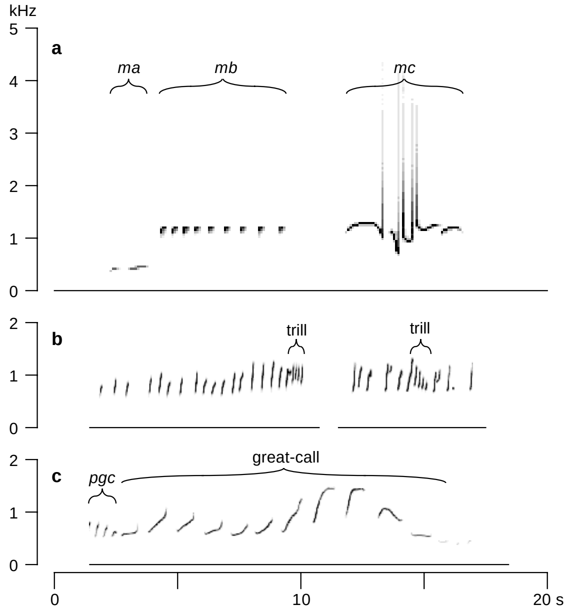

Fig. 5. Sonagrams (fundamental frequencies only) showing typical song phrases of the gibbon species examined for this study. (a) Male phrases of the northern white-cheeked crested gibbon (*N. leucogenys*). The sequence begins with booms (*ma*), followed by staccato notes (*mb*), and ends with a multi-modulated phrase (*mc*) (from Geissmann *et al.*, 2000). (b) Male phrases (two examples shown) of the Bornean gibbon (*H. muelleri*) (from Geissmann, 1993). (c) Female pre-great-call notes (*pgc*) followed by a great-call phrase of the agile gibbon (*H. agilis*) (from Geissmann, 1993). – *Sonagramme (nur Grundfrequenzen) von typischen Gesangsstrophen der Gibbonarten, die in dieser Studie untersucht wurden. (a) Männchenstrophen des Nördlichen Weißwangen-Schopfgibbons (*Nomascus leucogenys*). Die Sequenz beginnt mit Heullauten (*ma*), gefolgt von Staccato-Lauten (*mb*), und endet in einer multi-modulierten Strophe (*mc*) (aus Geissmann et al., 2000). (b) Männchenstrophen (zwei Beispiele) des Grauen Gibbons (*Hylobates muelleri*) (aus Geissmann, 1993). (c) Einleitungslaute (*pgc*) gefolgt von einer *great-call*-Strophe eines weiblichen Schwarzhandgibbons (*H. agilis*) (aus Geissmann, 1993).*

For the present acoustic analyses of *N. leucogenys* a series of staccato notes were investigated. The initial elements of the nine notes were analyzed in a sonagram, and spectral slices (Fourier transformations) were produced.

Males of *H. muelleri* typically produce short phrases of simple *wa*-notes and more complex phrases (Geissmann, 1993, Haimoff, 1985). The latter may include trills, quavering notes and various other note types in addition to *wa*-notes (Fig. 5b). The present analyses used a complex phrase consisting of simple *wa*-notes, *wa-oo-wa*-notes, and a trill. The initial six *wa*-notes before and the five *wa*-notes after the trill element were analyzed in sonagrams and spectral slices.

The most conspicuous song contributions of females of the species *H. agilis* (Fig. 5c) are known as great-call phrases and consist of long, frequency-modulated notes (Geissmann, 1993; Gittins, 1984; Haimoff, 1984a). Great-calls are typically preceded by a series of soft, short and simple *wa*-notes termed pre-great-call notes. The present analysis investigated the initial elements of a series of five pre-great-call notes.

Results

Sample 1: *Nomascus leucogenys* male

Figure 6 shows the sonagram of a staccato phrase of a male northern white-cheeked crested gibbon (*N. leucogenys*). A single staccato note can be transcribed as [wɑ]-[u:]. The intervals between consecutive staccato notes becomes longer from the beginning to the end of the phrase, and the harmonic structures appear to change from the more rapid articulation of the initial sound units to the more isolated notes at the end of the phrase. In order to test for ‘co-articulation’, the initial sound of each note was analyzed to determine whether the final sound of a preceding note was co-articulated with the succeeding sound.

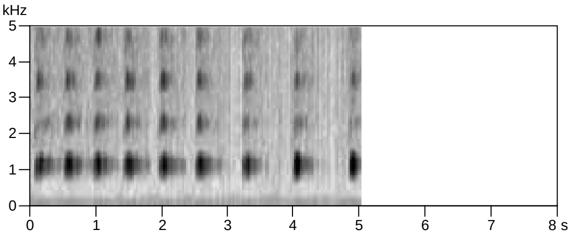

Fig. 6. Sonagram (sound frequency vs. time) of an excerpt from a male staccato phrase, showing nine consecutive staccato notes. – *Sonagramm (Frequenz vs. Zeit) von einem Ausschnitt aus einer männlichen Staccato-Strophe mit neun aufeinanderfolgenden Staccato-Lauten.*

My results show that when the animal utters a series of closely followed [wɑ]-[u:] notes, the [w]-sound at the beginning of the staccato note differs from [w]-sound individually articulated notes, suggesting that co-articulation occurs when staccato notes are uttered in rapid succession at the beginning of the phrase but not when they occur at longer intervals at the end of the phrase.

The comparison of the different [w]-varieties (co-articulated versus separately articulated) shows that when the [w] is co-articulated, the overtone structure gains in amplitude. In addition, the envelope curves display relative stable regularity. Two examples of these (i.e. of notes 3 and 4) are shown in Fig. 7.

Compared to co-articulated onsets of notes 3 and 4, non-co-articulated sound onsets of notes 8 and 9 show different envelope patterns, with respect to amplitude range and curve structure. Two examples of the latter are shown in Fig. 8.

In Fig. 7, the co-articulation of the initial [w] of the forth note with the final [ɑː] of the previous note suggests that the articulatory position of the final sound of the third note remains constant throughout the adjacent sound, a process resembling ‘co-articulation’ as described by Liberman *et al.* (1967).

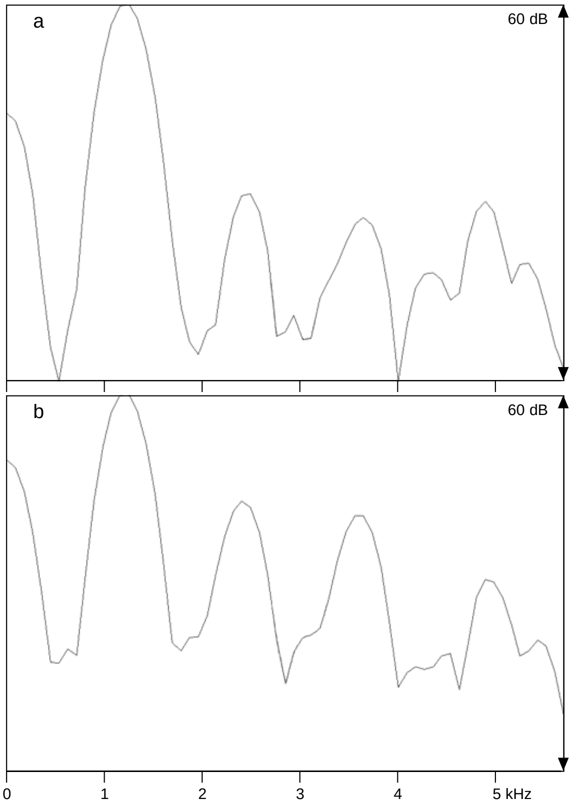

Fig. 7. Envelope curves of co-articulated [w]-onsets of staccato notes. (a): note 3; co-articulation occurs with note 2. (b): note 4; co-articulation occurs with note 3. – *Hüllkurven des koartikulierten Lautbeginns von Staccato-Lauten. (a): Laut 3; Koartikulation mit Laut 2 tritt auf. (b): Laut 4; Koartikulation mit Laut 3 tritt auf.*

When there was no ‘co-articulation’, i.e. when the notes were uttered with long pauses in between, the overtone patterns were different (Fig. 8). Notes 8 and 9 were both produced individually and separately from other notes, without co-articulatory influences. The spectral slices show that the envelope structure in those two (non co-articulated) [w]-sounds is largely the same, with the first envelope exceeding the upper overtones in amplitude and the overtones being structurally different from the co-articulated sounds shown in Fig. 7.

These dissimilarities in overtone structure between co-articulated and separately articulated notes cannot be attributed to practice-effects of song notes, since notes 8 and 9 were sung after notes 3 and 4. On the contrary, practising would produce more regular overtone-amplitude curves, which was not the case in these notes. The envelopes of the overtones were probably altered by co-articulatory effects.

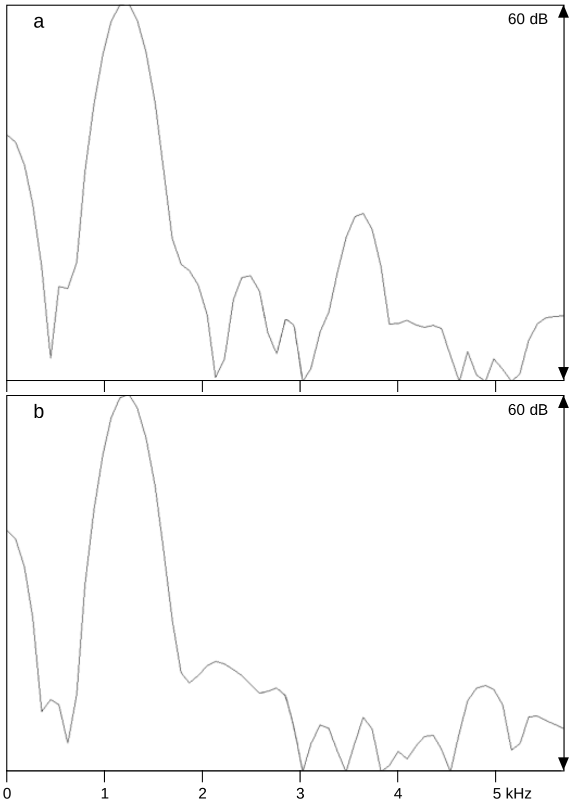

Fig. 8. Envelopes of [w]-onsets of staccato notes that were not co-articulated. (a): note 8. (b): note 9. – *Hüllkurven des nicht koartikulierten Lautbeginns von Staccato-Lauten. (a): Laut 8. (b): Laut 9.*

Sample 2: *Hylobates muelleri* male

The sonagram in Fig. 9 shows a complex phrase of a male Bornean gibbon (*H. muelleri*). It begins with six *wa*-notes uttered at long intervals; this is followed by two *wa-oo-wa*-notes and a short trill, and the phrase ends with five additional *wa*-notes uttered in more rapid succession.

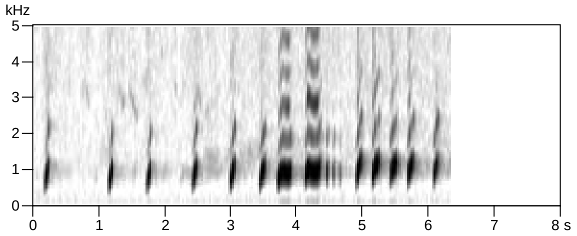

Fig. 9. Sonagram (sound frequency vs. time) of a male phrase consisting of a series of six *wa*-notes followed by a trill and more complex notes. – *Sonagramm (Frequenz vs. Zeit) einer Männchen-Strophe, bestehend aus einer Abfolge von sechs* wa-*Lauten, gefolgt von einem Triller und komplexeren Lauten.*

For this study, the onsets of each *wa*-note (before and after the trill) were analyzed. Based on the analysis of Sample 1 (see above), it was predicted that the male *H. muelleri* would show co-articulatory influences in *wa*-notes that are uttered in very close succession (i.e. the notes at the end of the phrase).

The comparison of the envelope curves reveals that the *wa*-notes uttered with long intervals before the trill are structurally different from the *wa*-notes that are produced at short intervals after the trill. In an individually articulated *wa*-note, the overtone structure displays low amplitude ranges and irregularities regarding the curves (Fig. 10a).

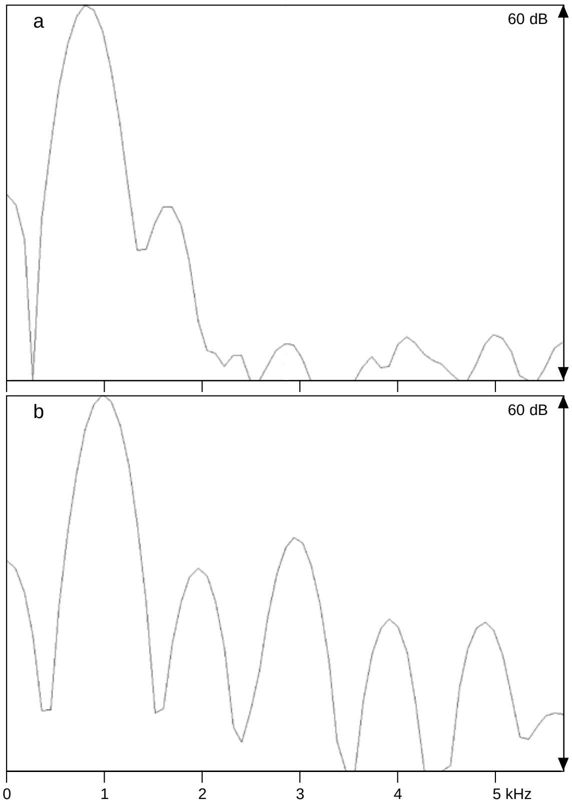

Fig. 10. Envelope curves of a [w]-onset of *wa*-notes that was not co-articulated (a) and of a co-articulated *wa*-note (b). – *Hüllkurven eines nicht koartikulierten Lautbeginns (a) und eines koartikulierten Lautbeginns (b) von* wa-*Lauten.*

When *wa*-notes are produced in close succession (shortly preceding the trill), the envelopes assume higher amplitude and more regularity (Fig. 10b).

This finding suggests that the structural differences in the overtones of the sounds result from co-articulatory influences occurring when the notes are uttered in rapid succession. A similar difference can also be observed when the *wa*-notes immediately following the trill at short intervals are compared to the *wa*-notes immediately following later, and at slightly longer intervals, after the trill (Fig. 9).

Sample 3: *Hylobates agilis* female

The sonagram in Fig. 11 shows five pre-great-call notes and the beginning of a great-call of a female agile gibbon (*H. agilis*). The notes that were analysed of this sample are the pre-great-call notes. Similar to the notes analysed of Sample 2, they sound like *wa*. This note series begins with long intervals and ends with shorter intervals (Fig. 11).

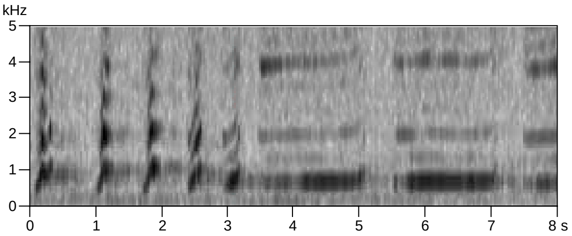

Fig. 11. Sonagram (frequency vs. time) showing an excerpt from a series of female pre-great-call notes followed by long, frequency modulated notes which represent the first notes of a great-call phrase. – *Sonagramm (Frequenz vs. Zeit) von einer Abfolge von* great-call-*Einleitungslauten eines Weibchens, gefolgt von den ersten langen, frequenz-modulierten Lauten einer* great-call-*Strophe.*

The spectral slices reveal differences in harmonic patterning between notes uttered at longer intervals (Fig. 12a) and notes that are uttered at shorter intervals (Fig. 12b), suggesting that this gibbon, too, produces envelope differences in notes according to co-articulatory effects occurring in notes uttered in rapid succession.

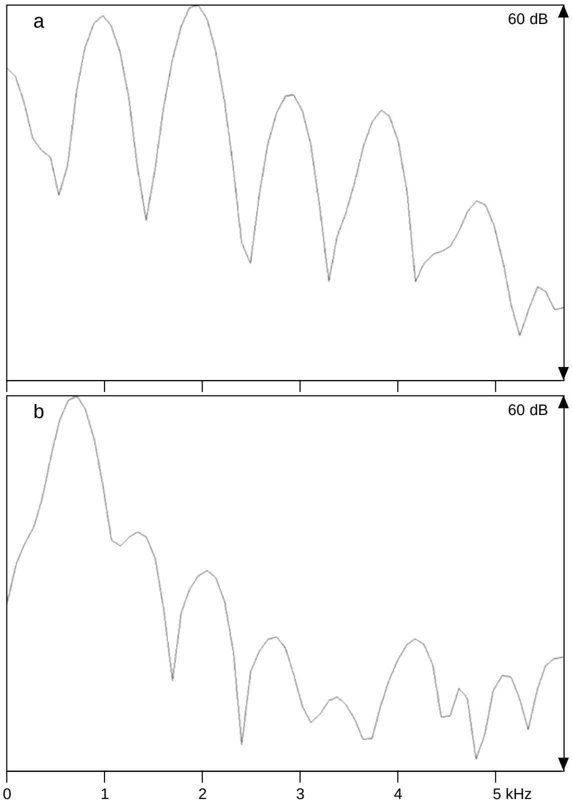

Fig. 12. Envelope curves of a [w]-onset of a note that was not co-articulated (a) and of a co-articulated note (b). – *Hüllkurven eines nicht koartikulierten Lautbeginns (a) und eines koartikulierten Lautbeginns (b) von* great-call-*Einleitungslauten.*

Contrary to the male notes of Samples 1 and 2, the notes of the female agile gibbon exhibit a tendency to be less stable when co-articulation occurs. The overtone structure in the female [w]-sound decreases in amplitude and shows more irregular patterning when co-articulated.

Discussion

A comparison of the different staccato notes of the male northern white-cheeked crested gibbon (*N. leucogenys*), shows that when song notes are uttered at long intervals, the upper harmonics are generally lower than when the sounds are produced at short intervals. This is revealed by the different spectral slices for the variations of the [w]-sounds that initiate each staccato note. This difference probably results from co-articulatory influences that occur when notes are uttered at short intervals.

The spectral slices of *wa*-notes of a male Bornean gibbon (*H. muelleri*) show a similar trend, with the envelope patterns displaying a more regular overtone structure and higher amplitudes when the notes are produced in rapid succession, whereas the harmonic structure is lower in amplitude and exhibits more irregular patterning when notes are articulated independently.

In the pre-great-call notes of a female agile gibbon (*H. agilis*), the trend described above is reversed. The female notes exhibit a more regular overtone structure when they are individually articulated, and co-articulation seemed to cause lower amplitude ranges and more irregular harmonic patterning in the overtones of the notes.

The above results suggest that differences in the spectral characters among song elements of all three study animals may be attributed to co-articulatory influences. In the onsets of male notes, the overtones become more stabilized and higher in amplitude when the notes are co-articulated, whereas an opposite trend appears to occur in the female notes. It has been well established that gibbon songs exhibit species-specific and sex-specific features (Geissmann 1993, 2002, Marshall and Marshall, 1976), as well as individual characteristics (Dallmann and Geissmann, 2001a, b; Geissmann *et al.*, 2005; Haimoff *et al.*, 1985a, b). Because of the small size of my samples, it is impossible to determine whether differences between them are related to species, sex, or individual, and even sample-specific influences cannot be ruled out. To resolve this question, further investigation using much larger samples is required.

The occurrence of co-articulatory influences on gibbon song notes might indicate that a mechanism closely resembling human ‘co-articulation’ is in place in gibbon vocalizations. The acoustic structures of note-onsets appear to be influenced by neighbouring sounds whose articulatory gestures overlap. Song notes of similar phonetic nature (e.g. “staccato notes”) can have different acoustic realizations in the investigated animals. This might suggest that the real percept of sounds is not the acoustic feature since it is unreliable. Gibbons, in a way similar to humans, could conceivably map between the acoustic signal and the vocal tract gesture. A listening animal may be able to perceive the “articulatory motor gesture” produced by a calling animal, since the acoustic signal itself does not sufficiently describe the sound.

According to Liberman’s ‘motor theory’, the perception of a sound activates similar brain regions as the production of the sound does, a claim that has been increasingly supported by research on the functions of mirror neurons (e.g. Rizzolatti and Craighero, 2004). The findings of the present paper provide indications that gibbons may perceive sounds as motor gestures and therefore map between production and perception processes that are involved in the sounds.

A shared production-perception network constitutes a very reliable system for the individual analysis and the inter-individual transfer of sounds and became increasingly more important with the advent of the large diversity and plurality of phonetic units that characterize human spoken language.

Acknowledgements

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Zusammenfassung

Eine „motorische Theorie der Laut-Perzeption“ für Primaten: Drei Fallstudien an Gibbons

Die „motorische Theorie der Sprachperzeption“ von Liberman *et al.* (1967) ist eine populäre neurolinguistische Theorie, welche die Verarbeitung von Sprachlauten (Phonemen) im Gehirn erklärt. Ein Phonem kann mehrere akustische Varianten haben, abhängig vom klanglichen Kontext, in den es eingebettet ist. Diese Beeinflussung eines Lautes durch den lautlichen Kontext wird als Koartikulation bezeichnet. So kann, zum Beispiel, das Phonem /g/ unterschiedliche akustische Merkmale aufweisen, je nachdem ob es in einem Wort von einem [i] oder einem [u] gefolgt wird. Manche Phoneme, die je nach Koartikulation physikalisch ganz verschieden sind, können wir auf Grund von Lernprozessen klanglich nicht mehr unterscheiden. Die akustischen Eigenschaften eines Phonems reichen demzufolge nicht aus, um den Laut zufriedenstellend zu beschreiben. Liberman *et al.* postulieren, dass die eigentliche Perzeption von Sprachlauten auf der artikulatorischen Geste, die der Produktion dieser Laute unterliegt, basiert. Somit wird /g/ nicht anhand der akustischen Eigenschaften wahrgenommen, sondern anhand der Sprachmorphologie, welche die Produktion des Lautes beschreibt (z.B. ist /g/ ein 'alveolarer Verschlußlaut'). Die Zuhörer ordnen das akustische Signal dem entsprechenden Artikulationshintergrund zu und verstehen dadurch den Laut.

Da Sprachlaute nicht als akustische sondern motorisch-artikulatorische Einheiten definiert werden, kommt es beim Sprechen zu Überlappungen der artikulatorischen Gesten, was von Liberman *et al.* als „Koartikulation“ bezeichnet wird. Sprache folgt somit nicht den Regeln eines akustischen Alphabets, in dem Laute chronologisch geäußert werden, sondern wird als ein „effizienter Code“ verstanden (Liberman *et al.*, 1967). Die assimilierten Laute können anhand ihrer stabilen und gleich bleibenden Artikulationsbasis identifiziert werden.

Jede Art von vokaler Kommunikation, die Koartikulation aufweist, kann vokale Einheiten nicht ausschließlich anhand ihrer akustischen Eigenschaften definieren, da diese instabil und deshalb unzuverlässig sein können.

Willams and Nottebohm (1985) konnten nachweisen, dass Liberman's „motorische Theorie“ auch auf Vogelgesänge angewandt werden kann. Es konnte gezeigt werden, dass Zebrafinken Töne wahrnehmen, indem sie diese in eine motorische Artikulationsgeste übersetzen. Das akustische Signal gibt Aufschluss über die ihm zugrunde liegende Vokaltrakt-Geste, die das eigentliche Objekt der Lautperzeption darstellt.

Der vorliegende Artikel versucht, die Liberman'sche Theorie der Sprachperzeption auf die Vokalisationen von Gibbons anzuwenden. Es wurden dazu Gesangsproben von drei verschiedenen Tieren unterschiedlicher Geschlechter und Arten untersucht, um koartikulatorische Effekte zu identifizieren. Die ausgewerteten Gesangsausschnitte stammen von je einem männlichen nördlichen Weisswangen-Schopfgibbon (*Nomascus leucogenys*), einem männlichen grauen Gibbon (*Hylobates muelleri*) und einem weiblichen Schwarzhandgibbon (*H. agilis*). Von den Tonausschnitten wurden Sonagramme und Hüllkurven erstellt, die Aufschluß über die akustischen Merkmale der Töne geben. Die Resultate erbringen erste Anzeichen dafür, dass die untersuchten Tiere Koartikulation in ihren Gesängen aufweisen. Das bedeutet, dass das akustische Signal in verschiedenen Ton-Umgebungen unterschiedlich sein kann und somit nicht der primären Definition von Lauten (für die Produktion und Wahrnehmung) dienen kann. Dies lässt vermuten, dass die artikulatorische Geste, die der Produktion der Laute unterliegt, eine Rolle in der Wahrnehmung spielt.

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Congresses and Workshops

4. Annual Meeting of the Gibbon Conservation Alliance

19 April 2008, Affenberg Salem, Germany

E-mail: info@gibbonconservation.org

Website: www.gibbonconservation.org

31th Annual Meeting of the American Society of Primatologists

18–21 June 2008, West Palm Beach, Forida, U.S.A.

Website: www.asp.org/meetings/index.html

22nd Kongress of the International Primatological Society

3–8 August 2008, Edinburgh International Conference Centre, Edinburgh, Scotland

E-mail: meetings@psgb.org

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3rd Congress of the European Federation for Primatology

12–15 August 2009, Zurich University, Switzerland

What is the Gibbon Conservation Alliance?

Gibbon Conservation Alliance

Goals

The **Gibbon Conservation Alliance** (GCA) supports the active conservation of gibbons, promotes research on their natural history, and raises awareness on gibbons and their plight. The **GCA** is a non-profit organisation. The **GCA** always welcomes help and funds to continue its important work.

Main Activities

- Publication of the Gibbon Journal and the Annual Report of the **Gibbon Conservation Alliance**
- Maintenance of a Website providing information on the **Gibbon Conservation Alliance** and its activities
- Raising funds to support gibbon conservation projects
- Promoting awareness of gibbons and the need to make efforts towards their conservation, as well as providing research results on gibbons. This can be carried out through lectures, publications, website, etc.

Organisation

The **Gibbon Conservation Alliance** is a non-governmental organisation based in Zurich/Switzerland. Established in 2004, the **Gibbon Conservation Alliance** comprises a small group of volunteers that raises funds for the conservation of gibbons.

How Can I Become a Member?

By becoming a member or by making a donation, you are helping us raise awareness and support for the conservation of the gibbons. An electronic application is possible via our Website (www.gibbonconservation.org). An application form can also be found on the last page of this publication. Additional application forms and information can be obtained from the following address: **Gibbon Conservation Alliance**, Anthropological Institute, University Zurich-Irchel, Winterthurerstrasse 190, CH–8057 Zurich, Switzerland; E-mail: www.info@gibbonconservation.org

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How can I help the Gibbons?

Application

In order to apply to the **Gibbon Conservation Alliance** for membership, please fill out this form and send it to: **Gibbon Conservation Alliance**, Anthropological Institute, University Zurich-Irchel, Winterthurerstrasse 190, CH–8057 Zurich, Switzerland. Please note that entries marked with a * are mandatory.

Annual membership fees: Regular Member CHF 30.–, Students CHF 20.–

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Thank you for helping us save the gibbons!