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Inheritance of Song Parameters in the Gibbon Song, Analysed in 2 Hybrid Gibbons (*Hylobates pileatus* × *H. lar*)

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Abstract. The song of a male and a female hybrid gibbon (*Hylobates pileatus* x *H. lar*) is described. Comparison with the song of both parental species revealed that at least some of the hybrid's song characteristics were inherited. Although several studies have tentatively suggested a genetical determination of gibbon song patterns, there have been no previous analyses of gibbon singing behaviour which conclusively documented this phenomenon. Attention is drawn to similarities between the song of the hybrids and gibbon species other than the parental ones, and their significance is considered.

Introduction

All gibbon species on which investigation has been carried out live in tropical rain forests, in monogamous, strictly territorial family groups [Carpenter, 1940; Chivers, 1972, 1974; Ellefson, 1968, 1974; Gittins, 1980; Gittins and Raemaekers, 1980; Kappeler, in press; Tenaza, 1975a; Tilson, 1979, 1981; Whitten, 1982a, b]. Their conspicuous vocalizations, mainly uttered at specifically established times of day, probably play an important role in territorial behaviour, and possibly also in the maintenance of pair and family bonds [for a list of references see Geissmann, 1983]. Among most gibbon species, mates vocalize together in a relatively rigid pattern, and at least in part, with a sex-specific repertoire so that a so-called duet evolves [Deputte, 1982; Deputte and Leclerc-Cassan, 1981; Geissmann, 1983; Gittins, 1978a; Goustard, 1979a, b, 1980, 1982a, b; Haimoff, 1981, 1984, in press a, b, c; Lamprecht, 1970; Marler and Tenaza, 1977; Marshall, 1981; Marshall et al., 1972; Marshall and Marshall, 1976; Schilling, 1980; Schröpel, 1977; Tembrock, 1962, 1964, 1974; Ziegler and Knobloch, 1968]. All gibbon songs show a similarly determined sequential structure [Haimoff, in press a; Haimoff et al., 1982]. This includes solo songs of those species where, up to now, no duets have been described in the wild [Kappeler, in press, pers. commun.; Marler and Tenaza, 1977; Tenaza, 1975b, 1976; Whitten, 1982c].

The song repertoire is notably constant in structure and organization for each species, and according to several authors believed to be largely genetically determined [Boutan, 1913; Brockelman, 1978; Carpenter, 1940; Marler and Tenaza, 1977; Tembrock, 19701. However, proof or disproof of inherited song characteristics could not be conclusively determined from previous research. The observation that captive gibbons retain their species-specific song even in heterogenous groups [Carpenter, 1940] does not explain how these animals acquired their particular song. Boutan [1913] raised a young gibbon in isolation from other gibbons; also this animal finally could utter (according to Boutan) the song typical of this species. The possibility cannot be precluded, however, that this animal learned the song from his parents prior to separation; moreover, it is not clear from this otherwise detailed description, to what extent the song of this animal was in fact species-specific.

There remains the question of how the species-specific song traits can be passed on from one generation to the next. Critical evidence could, under particular circumstances which exclude the possibility of parental teaching, be expected from the analysis of songs from hybrid gibbons compared with their parents. In fact, several gibbon species have been crossed in captivity (see e.g. the records of ‘mammals bred in captivity’, in: Int. Zoo Yearbook, 1962-1974, 1977-1981); the most spectacular case describes a gibbon-siamang hybrid, *H. muelleri abbotti* x *H. syndactylus* [Myers and Shafer, 1979; Rumbaugh et al., 1976; Wolkin and Myers, 19801. In addition, from several species with adjoining or overlapping distribution, individual feral hybrids have been reported [Brockelman, 1978; Gittins, 1978b].

Nevertheless, only fragmentary details are available regarding the songs of gibbon hybrids. Brockelman [1978] reports ‘odd vocalizations’ in connection with naturally occurring hybrids between *H. lar* and *H. pileatus.* Marler and Tenaza [1977] describe a pair of *H. lar* x *H. muelleri* hybrids where the females’ song was ‘structurally intermediate between songs of the parental species’, whereas ‘both song structure and duetting behavior’ of the male hybrid resembled that of the father. One should note that in the description of hybrids presented here, the father’s species is mentioned before the mother’s. Maples and Haraway [1982] stated that a female *H. muelleri* x *H. agilis* hybrid vocalized in a way that was typical for *H. muelleri* females, and ‘quite different from the song of either of her parents’. The authors claim, moreover, that the daughter produced this song without ever having heard it before.

Hybrids such as those examined here, namely crosses between the pileated or capped gibbon, *H. pileatus*, and the *lar* or white-handed gibbon, *H. lar*, have been repeatedly born in captivity and have become the object of scientific studies [Ibscher, 1964, 1967; Meyer-Holzapfel, 1950; Steiner, 1949]. Backcrosses have also been reported [e.g. Groves, 19721. The distribution of both parental species overlaps slightly in the area of Khao Yai National Park in northeast Thailand, about 200 km northeast of Bangkok [Marshall et al., 1972]. There, several mixed pairs and hybrids were observed [Brockelman, 1978].

Whereas few exact details on vocalizations of these hybrids are available as yet, the songs of the parental species have been described by several authors and, to some extent, documented with sonagrams [e.g. see for *H. lar*: Caldecott and Haimoff, 1983; Carpenter, 1940; Chivers, 1974, 1978; Ellefson, 1974; Haimoff, in press a; Marler and Tenaza, 1977; Marshall, 1981; Marshall et al., 1972; Marshall and Marshall, 1976; Schröpel, 1977; Tembrock, 1974; for *H. pileatus*: Brockelman, 1975; Geissmann, 1983; Haimoff, in press a; Marler and Tenaza, 1977; Marshall et al., 1972; Marshall and Marshall, 1976].

Since the following study is based on the very limited material of one song of a male and a female hybrid, the complete span of variation cannot be described, nor can statements about the songs' structure be conclusively generalized. However, it can be shown for the first time whether some of the song characteristics passed on from parent to hybrid are based on genetic or learned processes (where the latter implies learning from the parents).

Animals and Methods

One song of 2 gibbon hybrids, H. pileatus x H. *lar*, was analysed for purpose of this study. Both animals, a 6-year-old male (born 5.11.1975) and a 12-year-old female (born Nov. or Dec. 1969) were kept together with their mother (*H. lar*, pale 'phase') and a third hybrid (3.5 years old, born 3.3.1978) as a group in the Opel Zoo in Kronberg (FRG). All 3 aforementioned hybrids are full brothers and sisters and were raised by their mother. The hybrids' father (*H. pileatus*) was given to the Zoological Garden in Zürich on March 9, 1981. Actual sexual behaviour was not observed among these animals. However, the hybrid female was so oppressed at times by her brother and her father that she would crawl under the bridge from the interior of the cage to the exterior island, to bring herself to safety [*Jantschke*, pers. commun.].

The song analysed in this study was tape recorded on September 21, 198 1, and lasted 5.4 min. The mother, daughter and eldest son participated in a trio song. In order to compare, songs of both parental species were tape recorded in Switzerland (Zoological Garden Zürich, Zoo Seeteufel/Studen, Zoo Al Maglio/Magliaso, Knie's Kinderzoo / Rapperswil) and in France (Zoological Garden Mulhouse). The recordings of *H. moloch* were made at the Zoo Hellabrunn/München.

To determine the species-specific length of phrases and the number of notes per phrase, data and sonagrams of the following authors were consulted: Caldecott and Haimoff [1983], Chivers [19741, Chivers and Gittins [1978], Haimoff [in press a], Kappeler [in press], Marler and Tenaza [1977], Marshall et al. [1972], Marshall and Marshall [1976], Schr8pel [1977], Srikosamatara [19831, as well as the song excerpts collected on disc by Marshall and Marshall [1978].

The examples of phrases sung by the *pileatus* male in figure 3 stem from the father of both hybrids here under analysis. Further sonagrams of the same male were demonstrated by Geissmann [1983].

Vocalizations were recorded with an UHER 4200 Report Stereo tape recorder (with tape speed of 9.5 cm/s) and an AKG directional microphone (model CK9). The sonagrams were produced with the Ubiquitous Spectrum Analyzer UA-500A (Nicolet Scientific Corporation) and the camera Recordine.

In order to set off against each other the song contributions of several simultaneously vocalizing individuals, a new technique for the presentation of sonagrams was developed in collaboration with Mr. H. Rüegg. Formerly, the usual procedure of marking notes of different individuals was done by using additional ordering signs. This method had the disadvantage of easily producing unclear presentations, when notes of several individuals overlapped. The newer method introduced here avoids this difficulty, in that notes of individual gibbons can immediately be distinguished and attributed by their shade of grey. This method has an additional advantage in that the sonagrams are not altered by tracing and therefore retain their complete store of information.

To this end, on each of 3 identical sonagrams of the same trio song, contributions of 2 individual animals were covered with white coloration so that on each sonagram only the notes of 1 of the 3 would be visible. The 3 sonagrams were separately scanned and digitized at the IBM research laboratory in Zürich. Further processing was continued on an IBM 3083 mainframe computer using algorithms devised by the Digital Image Processing research group. First, a different grey level was attributed to each picture. Then, the 3 sonagrams were merged upon one another into their exact original positions. To make the sonagram richer in contrast, a grey background was generated. The final picture was presented through an electro erosion printer on black paper coated with an aluminium film. In this procedure, the metal-layer was selectively burned away from the paper by electrodes. The resolution of the outprint corresponds to 576 points/mm2. In the final picture, the song parts of separate individuals can be recognized by their varying grey levels.

A similar result had already been won through a photographic procedure developed by H. Kacher to demonstrate bird duets [Wickler and Uhrig, 1969].

The non-parametric statistical test methods are adapted from Siegel [1956] and all used two-tailed.

The duet songs of the various gibbon species show a similar arrangement of distinct sequences which differ in structure and organization: Most songs will begin with an ‘introductory sequence’ performed only once; thereafter the songs will consist of ‘organizing sequences’ and ‘great-call sequences’, produced in alternating succession [Haimoff, in press a; Haimoff et al., 1982].

Since all 3 animals participated in the introductory sequence and the first following organizing sequence, and since their notes followed each other very quickly, not all notes could be attributed with certainty to a specific individual. This study is therefore limited to describing the organization and note repertoire of the great-call sequences. In addition, contributions of the male (but not of the 2 females) to the organizing sequences will be analysed.

In accordance with questions posed in the introduction, song characteristics will be favoured for analysis in which the hybrid varies significantly from at least one of the parental species.

Results

In the hybrid songs analysed in this study, clear alternating order of organizing sequences and great-call sequences could be established. This song construction corresponds to the pattern typical for other gibbon songs, and was already described for both parental species by Haimoff [in press a] and Haimoff et al. [1982].

The song contributions of the male hybrid were composed of two note types, which can be described phonetically as ‘*wa*’ and ‘*aa*’ notes (borrowing the terminology from Haimoff [in press a]). The *wa* notes are generated by exhaling, as could be seen by the visible movements of the chest. The mouth is opened during the utterance, and the sound frequency climbs steeply. The basal frequency fluctuated between 600 and 800 Hz. The *aa* notes are produced by an inspiration and are situated between 800 and 1,000 Hz, approximately one fifth higher than the beginning of the *wa* notes.

The organizing sequences were primarily composed of note utterances from the hybrid male. His vocal contributions to these song sections consisted of a few single notes (wa notes), but primarily of phrases (see fig. 1). Here a phrase is defined as note sequences coming from 1 animal, separated from each other or from the next vocalization by an arbitrarily established interval of at least 2 s. The phrases in the organizing sequence had a median length of 9.67 s (range 2.21-14.73 s, n = 10), consisted of a median 16.25 notes (range 3-24, n = 7) and lay in the range of median 4.95 s from each other (range 2.1812.90 s, n = 11). All phrases that could be subjected to analysis began with a *wa* note and ended with a *wa* note (with one exception: one phrase ended on *aa*).

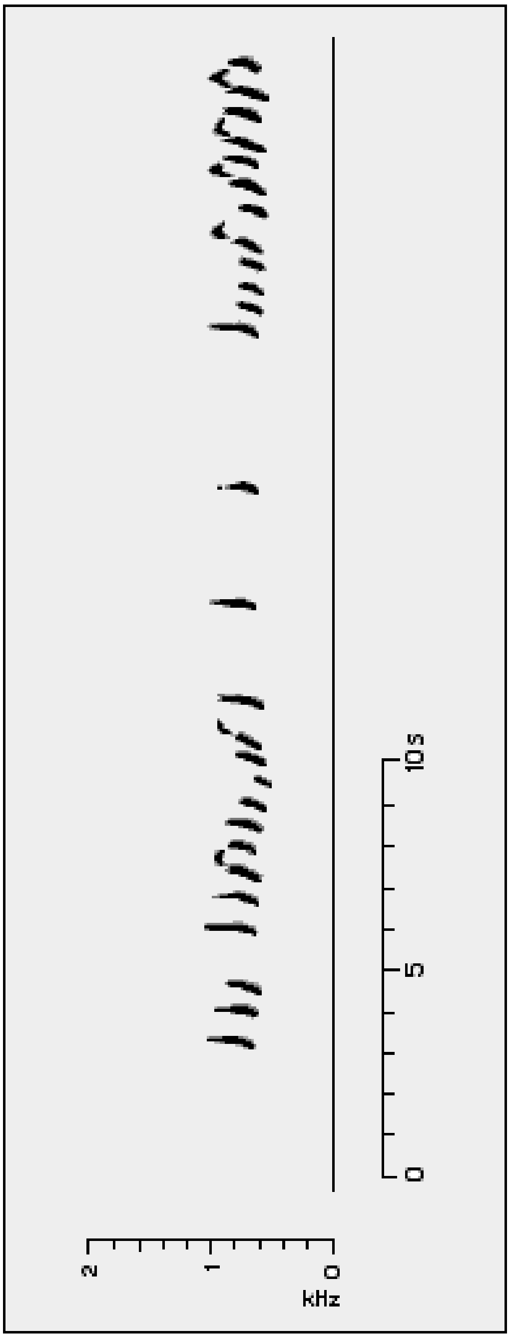


Fig. 1. Two phrases and two separate *wa* notes out of an organizing sequence of the male hybrid, *H. pileatus* x *H. lar* (Opel Zoo / Kronberg, 21.9.1981).

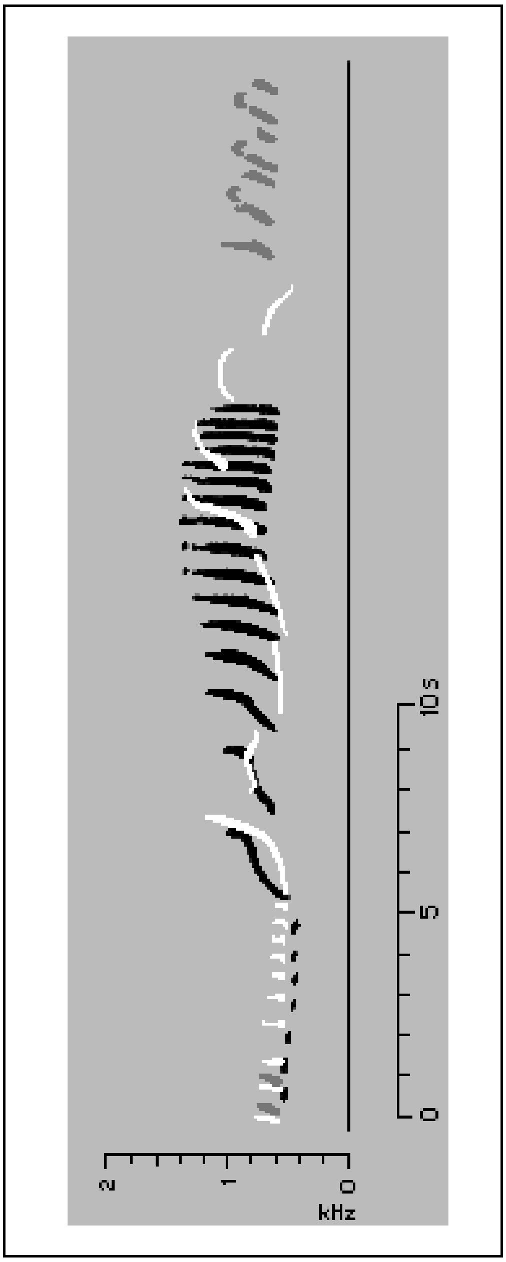


Fig. 2. Complete great-call sequence from the trio song of the 2 gibbon hybrids, *H. pileatus* x *H. lar*, and their mother, *H. lar* (Opel Zoo / Kronberg, 21.9.1981). White sonagrams: *lar* female; black sonagrams: hybrid female; dark grey sonagrams: hybrid male.

In addition to serially produced *wa* notes (*wa-wa* combinations), there occurred in male phrases also *wa-aa* and *aawa* combinations, but no *aa-aa* combinations. In order to test whether or not the succession probability of notes differed from random distribution, that is, whether certain note combinations were really preferred, the frequency with which each note followed each combination was computed. The results were that in actually 27 cases a *wa-aa* combination was followed by a *wa* note, but in no case by an *aa* note. This succession probability deviates significantly from simple random distribution ($p < 0.001$, chi-square test). Likewise, in 24 cases an *aa-wa* combination was followed by a wa, but never by an *aa* note. This deviation from random distribution is also significant ($p < 0.001$, chi-square test).

The observed succession probability cannot be explained through a repetition of simple two-note combinations, if both the *wa-aa* and the *aa-wa* combination are followed by wa, but not by *aa* notes. As the *aa* notes occur exclusively after a wa note and are followed by a wa note, the succession probability of notes is most likely to be attributed to a basic combination of three notes, namely the *wa-aa-wa* combination. This combination was found in 9 out of 10 phrases and occurred 26 times altogether (median 3 times per phrase, range 0-4, n = 10). This basic combination will here be designated a motif according to Thielcke's [1961] definition (but also corresponds to the term 'figure' in Haimoff [in press a]). All male phrases were, then, built upon series of wa notes and the motif described; only in one instance was the motif incomplete at the phrase's end (the last note was missing). A typical phrase could therefore sound like: '*wa wa wa wa-aa-wa wa-aawa wa-aa-wa*'.

The hybrid female fell twice into song with low, rhythmic *wa* notes of about 0.5 kHz (so-called 'opening notes' [Marshall and Marshall, 1976]; 'pre-great-call notes' [Haimoff, 1984]) and so led into the end of a specific organizing sequence and the beginning of a great-call sequence (see fig. 2). The actual great-call of the hybrid female begins with loud, long-drawn notes, with slowly rising frequency at the beginning of each note (flat branch in sonagram), but rising sharply toward the note's end (steep branch). During the first 2-3 notes ('soaring notes' [Marshall and Marshall, 1976]; 'introductory notes' [Haimoff, in press a]), the pitch increment of the flat branch surpasses that of the steep branch. These notes have a median duration of 1.6 s (range 1.2-1.8 s, n = 5) and show a median pitch increment of 0.43 kHz (start frequency: median = 0.60 kHz, range 0.50-0.63 kHz; end frequency: median = 1.03 kHz, range 0.93-1.03 kHz; n = 5). The note succession is progressively accelerated in that the flat branch is increasingly shortened, in that the steep branch grows increasingly steeper (and higher) and in that the intervals between the notes become shorter. The notes now have a median frequency climb of 0.67 kHz (start frequency: median = 0.60 kHz, range 0.53-0.73 kHz; end frequency: median = 1.33 kHz, range 1.07-1.40 kHz; n = 26). The rhythm becomes stabilized during the last 3-6 notes, at approximately 2.5 notes/s.

The entire great-call of the hybrid female had a median length of 12.0 s (range 11.5-12.6 s, n = 2) and consisted of 15.5 notes (range 15-16, n = 2). Whereas the mother of the hybrids sang a first great-call alone, the following great-calls were sung synchronously by both females; that is, both animals started the great-call simultaneously, but the hybrid female ended it earlier. The great-call of the *lar* female (see fig. 2) lasted a median of 14.3 s (range 14.0-14.6 s, n = 3).

The hybrid male ceased to vocalize during the pre-great-call notes and was silent during the entirety of the great-calls. Only after an interval of several tenths of a second (median = 0.98 s, range 0.80-1.34 s, n = 3) following the mother's great-call, he added an own phrase ('coda' [Haimoff, in press a, 1984; Marler and Tenaza, 1977; Marshall and Marshall, 1976]). Thus, a simple duet, or trio, respectively, developed (see fig. 2). The male's coda phrases only lasted about half as long (median = 4.18 s, range 3.93-4.45 s, n = 3) as his phrases during the organizing sequences (see above). In comparison to the latter, the coda phrases also contained fewer notes (median = 9.75, range 9-10, n = 3). However, they showed the same note inventory, and the same characteristic motif.

Discussion

Vocal differences between the hybrids examined and the parental species will be discussed in the following passages. To make comparison easier for the reader, sonagrams with representative song selections from the parental species have been arranged in figures 3 and 4.

The species-specific song characteristics of *H. lar* and *H. pileatus* were not found in the song of the F1 hybrid generation: Neither the typical short trills of the *pileatus* male ('short low bubbly trill' [Brockelman, 1975]; 'trill' [Chivers, 1977; Chivers and Gittins, 1978]; 'short bubbling sound' [Haimoff, in press a]; 'short bubbling roll' [Marshall et al., 1972]) nor the typical vibrato notes of the *lar* male ([Tembrock, 1974, 1977, 1978]; 'quiver hoots' [Chivers, 1977; Chivers and Gittins, 1978]; 'quiver notes' [Haimoff, in press a].; 'quavering notes' [Marshall et al., 1972; Marshall and Marshall, 1976]) could be established in the hybrid song. Nor could either the long held trills in the great-calls of *H. pileatus* ('long bubbly trill' [Brockelman, 1975]; 'rich bubbling call' [Chivers, 1977]; 'long rich bubble' [Chivers and Gittins, 1978]; 'prolonged bubbling' [Haimoff, in press a].; 'protracted, steady bubbling' [Marshall et al., 1972; Marshall and Marshall, 1976]), or the double rise and fall of pitch in the great-call of *H. lar* be established [Chivers, 1974; Chivers and Gittins, 1978; Haimoff, in press a; Marshall and Marshall, 1976].

However, only a very limited meaning can be attached to these negative findings, considering the scarce sampling of one hybrid song. For instance, in the male song of feral hybrids, Marshall (pers. commun.) found short trills which, however, were of slower rhythm than those of *H. pileatus*.

The combination of inhaled and exhaled notes as motifs of the hybrid male represents no newly observed trait, for it is characteristic of several gibbon species [Chivers, 1977; Chivers and Gittins, 1978; Haimoff, 1984, in press a; Marshall et al., 1972], such as for one of the parental species, namely *H. pileatus*. It is not, on the other hand, considered typical for *H. lar* [Marshall, 1981]. One would assume that the use of such a motif by *H. pileatus* and the hybrid male demonstrates a homologous characteristic that was transferred to the first hybrid generation from the father's (pileatus) side. Since the hybrid male could listen to his father for several years, it is not clear to what extent this transfer was caused by genetic or learned processes.

The 'switching on' of inhalation notes may have led to the fact that *H. pileatus* males emit more notes per phrase-second (median = 3.14, range 1.92-4.49, n = 38 phrases from 6 individuals) than males of *H. lar* (median = 1.67, range 0.83-2.54, n = 98 phrases from 10 individuals). The difference within this index is statistically significant ($p < 0.00003$, Mann-Whitney U test). The number of notes per phrase-second produced by the hybrid male (median = 1.96, range 1.36-2.55, n = 10 phrases) is between the values of the parental species, and is significantly different from the number of notes produced by *H. pileatus* ($p = 0.00006$), but not from that of *H. lar* ($p = 0.095$).

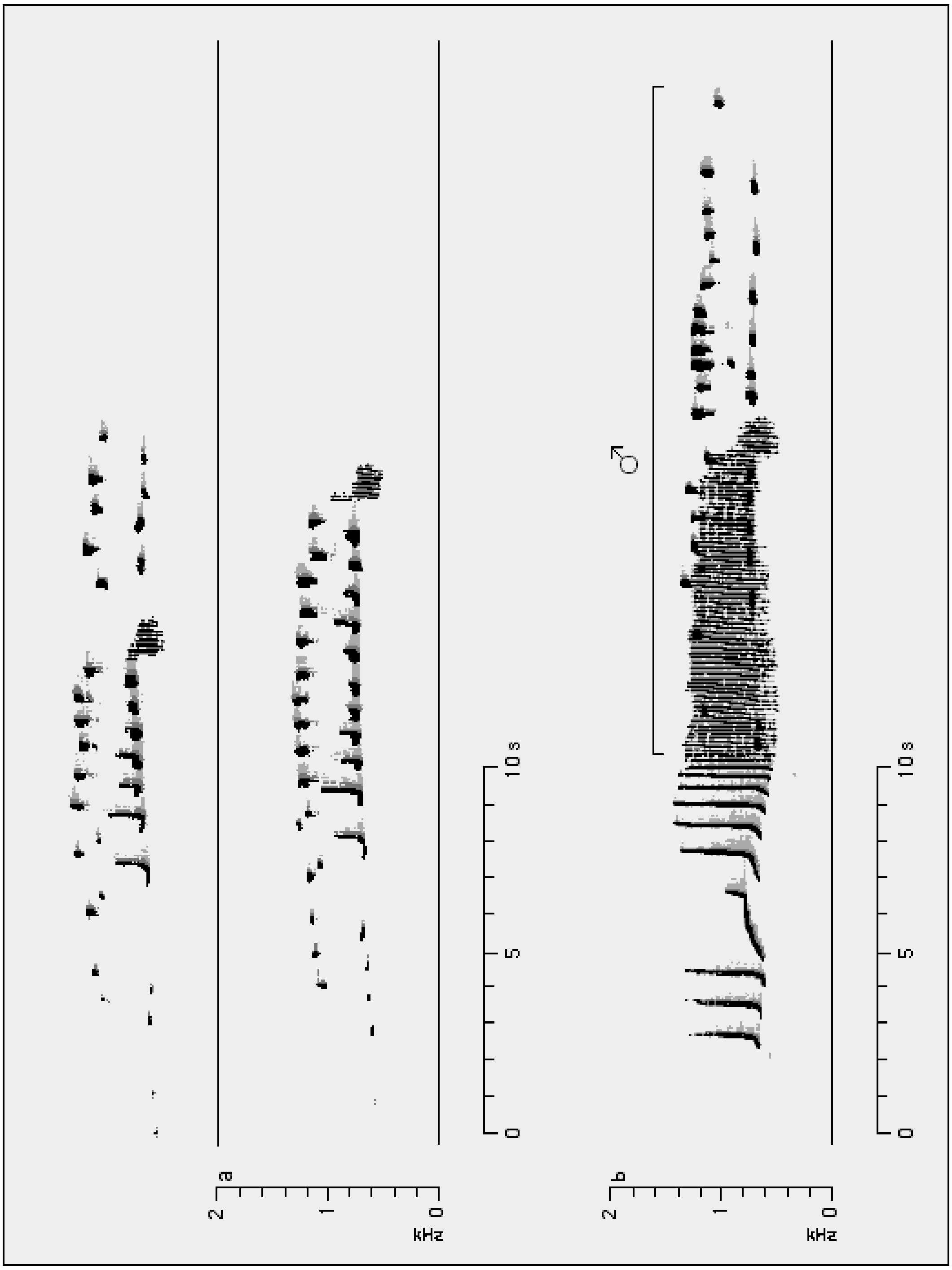
This difference could derive from the fact that in the male phrases of *H. pileatus* there is a regularly occurring characteristic trill that was not found in the song of the hybrid male evaluated here. This trill could explain why the index of *H. pileatus* shows a higher value than that shown by *H. lar* and by the hybrid male. If, on an experimental basis, a trill is reckoned as only one note, the index of *H. pileatus* actually sinks considerably (median = 2.08, range 1.41-3.70, same sample as above). Though there is still a significant difference to the index of *H. lar* ($p < 0.00003$, Mann-Whitney U test), there is no longer a significant difference to the hybrid male's index ($p = 0.0574$). The considerable discrepancy, then, in the index of *H. pileatus* and the hybrid male may be explained by the fact that the latter uttered no trill.

The exhaled notes in the phrases generated by the hybrid male begin at about 0.6 kHz and climb steeply to about 0.8 kHz. Such ascending notes are again typical of the male phrases produced by a large number of gibbon species including those of *H. lar*, but not by *H. pileatus*. With *H. pileatus* the expiration notes (*hoo* notes [Haimoff, in press a]) of the male motif (*hoo-aa* combination) are of a fairly constant pitch. The climb in pitch demonstrates, then, a trait that probably came from the mother's (*lar*) side into the hybrid motif. In that such notes are also uttered by *lar* females [Caldecott and Haimoff, 1983; Haimoff, in press a; own observ.], again nothing can be said about the extent to which learning and/or genetic processes are responsible for the transfer of this characteristic.

It is an interesting fact that the combination of an ascending expiration note followed by an inspiration note (which forms part of the wa-aa-wa motif described in the song of the hybrid male) appears in almost identically sounding form in the song of another species, the agile or black-handed gibbon, *H. agilis*: The wa-aa combination as part of a two part motif represents in this species an actually specific characteristic in the song of both sexes [Chivers, 1974, 1977; Haimoff, 1984; Marshall, 1981; Marshall et al., 1972; Marshall and Marshall, 1976]. As an ingredient of a three part motif, the *wa-aa* combination has, to my knowledge, not yet been described or even considered typical for any gibbon species.

Fig. 3.a Two typical male phrases out of an organizing sequence of *H. pileatus* (Zürich Zoo, March 198 1). The two sonagram lines are not to be read continuously. **b** Complete great-call sequence (duet) of a pair of *H. pileatus* (Zürich Zoo, 28.3.1981). The great-call of the female overlaps with the accompanying male phrase (coda).

Fig. 4.a Two typical male phrases and separate wa notes out of an organizing sequence from a pair of *H. lar* (Knie's Kinderzoo/Rapperswil, 17.6.1981). The two sonagram lines are to be read continuously. **b** Complete great-call sequence (duet) of a pair of *H. lar* (Zoo Seeteufel/Studen, 6.7.1981). The great-call of the female does not overlap with the accompanying male phrase (coda).



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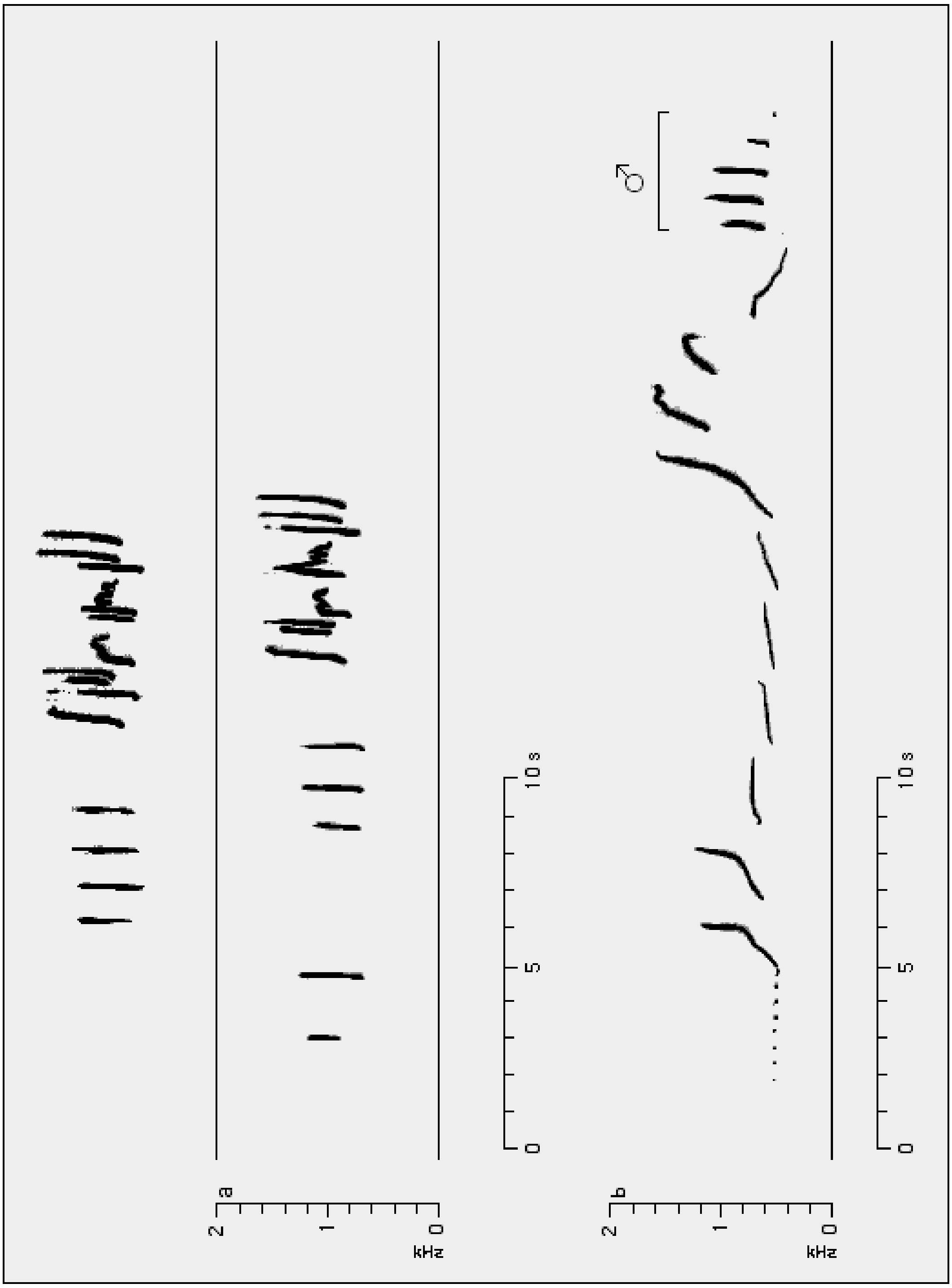

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Only 1 case is known to me where an adult female, supposed to be a pure *H. lar*, rarely uttered single wa-aa-wa combinations similar to the hybrid motifs described here. However, according to Marshall (pers. commun.) the three-parted motif occurs frequently in the songs of *H. agilis*. The consequent use of this motif in the phrases of the hybrid male cannot simply be explained by pointing to combinations of song characteristics possessed by the parental species. Since no 'exterior model' existed from which this motif could have been learned, the explanation must in this case lie with a genetically determined characteristic that only manifested itself phenotypically in the hybrid. I presuppose, however, that this motif is not an individual trait that has been acquired newly and independently from hybridization. The validity of this assumption can, however, only be verified in the presence of further hybrids' songs. At least the fact that here the hybrid male analysed shows certain similarities to the *agilis* male does not appear to be an individual phenomenon. In his work among feral gibbons, Brockelman (pers. commun.) also found among several hybrid males (one of whom a certain Fl hybrid) motifs which resembled those of *H. agilis.*

The typical song contribution of all gibbon species females contains, among others, a very 'standardized' phrase that can be precisely defined: the great-call. As opposed to the so-called pre-great-call notes, and the first soaring notes (both of which may sound very much alike among several gibbon species), particularly the following development of great-call notes shows clear inter-specific differences [e.g. Marshall and Marshall, 1976]. Whereas the pre-great-call notes of the hybrid female are again similar to those of both parental species, and while the first long drawn soaring note might still be classified within the variation span of the *H. lar* great-calls, we can see at the latest by the second long note that the great-call produced by the hybrid female does not run according to her mother's schema. Rather, the notes reveal a structure far more similar to the great-calls of *H. pileatus*: that is, they ascend in pitch and consist at the start of the great-call of a flat and steep branch. In the great-call of *H. lar* on the other hand, notes of completely different pitch modulations are used, among which there are not only ascending, but also descending notes. The hybrid female could not have learned the sequence of *pileatus* typical notes from her mother (*H. lar*), and no *pileatus* female was present as a model. This has to be considered a characteristic which, at least in this case, only could have been transferred to the hybrid generation on a genetical basis.

The development of a continual *acceleration* in the great-call is typical for various gibbon species [see e.g. Marshall and Marshall, 1976], such as for *H. pileatus*, but not for *H. lar*. Likewise, the hybrid female can never have heard a corresponding model, since only her father belonged to the species *H. pileatus*.

The point where the great-call's highest pitch, intensity, or speed is reached has been described as the 'climax' [e.g. Marshall and Marshall, 1976]. Whereas the great-call of *H. pileatus* and the hybrid female closely resemble each other in single notes and the acceleration of following ones, the climax never reaches the fast rhythm of notes (trill) of this parental species, where the individual notes follow another with such rapidity that the human ear does not perceive them as separate sounds. In the case of the hybrid female, the tempo of the note succession stabilizes at a much slower

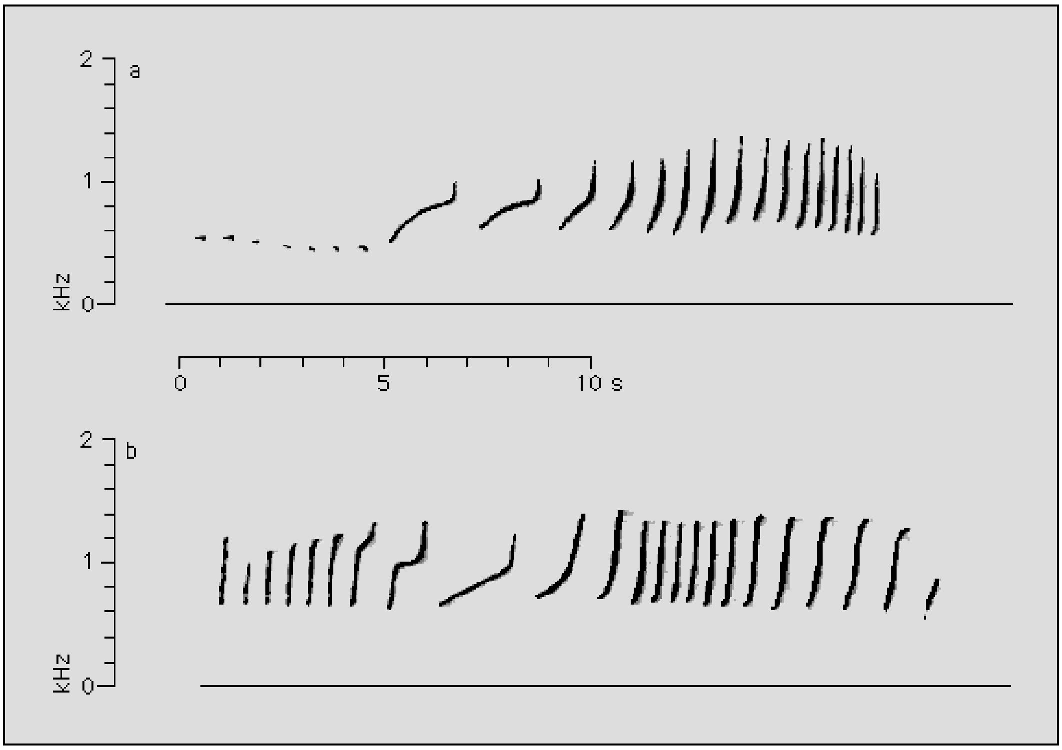

Fig. 5. a Great-call of the hybrid female (*H. pileatus* x *H. lar*). For this figure the same sonagram was used as for figure 2. From the original trio, the notes of the remaining participants are covered up. **b** Great-call of *H. moloch*. The recording on which this sonagram is based was made in the wild (W.-Java) by Dr. J.T. Marshall, and is contained on the disc 'The Gibbons' [Marshall and Marshall, 1978].

rhythm. However, since also the note rhythm in the climax of the great-call does not correspond to that of the mother or *H. lar* in general, it must be under at least partial genetical control from the side of *H. pileatus*.

Interestingly, this great-call that is developed through hybridization more closely resembles that of *H. moloch* in terms of general structure and organization than that of the parental species involved; one should compare the great-call sonagrams presented in figures 3 and 4 with figure 5. The pre-great call notes would not be considered here as part of the great-calls. The median number of notes per great-call lies at 9.5 (range 7-16, n = 67 great-calls from 13 individuals), for *H. lar.* For *H. pileatus*, on the other hand, a median value of 83 notes was determined (range 63-109, n = 20 great-calls from 5 individuals). The corresponding value for the hybrid female is 15.5 (range 15-16, n = 2), and lies between the values of both parental species, somewhat closer to *H. lar*, and still closer to the value computed for *H. moloch* (median = 14.6, range

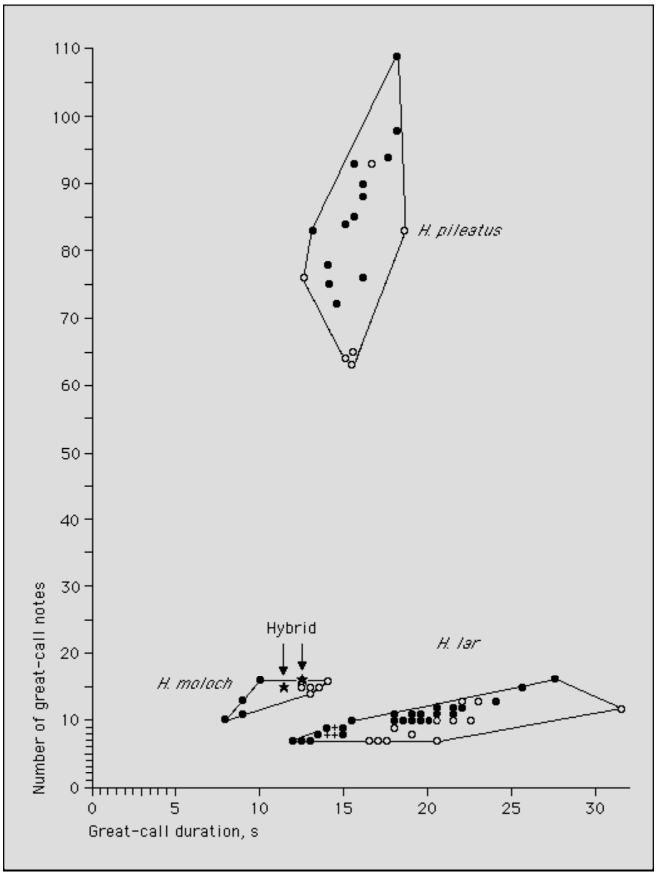

Fig. 6. The number of notes in a great-call plotted against its duration. Each point or circle corresponds to a great-call; some of these points overlap. The points identify own recordings, while the circles correspond to literary data (see 'Animals and methods'). The constellations of the three analyzed species are encompassed with the shortest possible enclosure line. The resulting polygons do not overlap; the two plotted song characteristics are therefore sufficient to separate these females of the three species clearly from one another. The values of the hybrid female (*H. pileatus* x *H. lar*) are identified with a star. One should observe that they lie outside of the constellations of both parental species, but within the constellation of *H. moloch.* The values for the mother of the hybrid female are shown as crosses.

10-16, n = 13 great-calls from 6 individuals). The same is true for the duration of the great-call. Here again the value of the hybrid female (median = 12.0 s, range 11.5-12.6 s, n = 2) is closer to *H. moloch* (median = 12.4 s, range 7.9-14.0 s, n = 13 great-calls from 6 individuals) than to the parental species *H. pileatus* (median = 16.4 s, range 12.7-20.0 s, n = 21 great-calls from 7 individuals) and *H. lar* (median = 19.2 s, range 12.0-31.3 s, n = 64 great-calls from 17 individuals). The values for the separately analysed great-calls are shown in figure 6.

The correspondence in song structure of the female hybrid and *H. moloch*, as examined here in the great-call, does not seem to be simply the result of individual trait combinations in this particular hybrid. Brockelman and Marshall (both pers. commun.) actually confirmed similar correspondences to the great-call of *H. moloch* in several feral hybrids between *H. lar* and *H. pileatus*.

It should be noted that the duration of the hybrid female's great-calls lies clearly under the corresponding median values of both parental species (table I), but still within the

Table I. Index of the relation between number of notes and duration of the great-call in various gibbon species and in the hybrid female analysed

	Median number of notes per great-call	Median duration of great-call, s	Median index of number of notes per duration
H. lar	9.5	19.2	0.53
H. pileatus	83.0	16.4	5.52
H. pileatus x *H. lar*	15.5	12.0	1.29
H. moloch	14.6	12.4	1.25

lower bounds of their range of variation. Since the value of the hybrid female is only slightly under that of her mother, the shortness of the great-calls should not necessarily be seen in connection with hybridization, but rather in terms of individual variability.

The index of the proportion between number of notes and length of the great-call brings these absolute figures to a more easily comparable measure which is also indicative of the overall note rhythm in the great-call (see table I). Also in this index figure the hybrid female is in an intermediate position between the corresponding values of the parental species, but at the same time even closer to *H. moloch.* Since the hybrid female is *in* an intermediate position between the two parental species with regard to overall note rhythm as well as length of the great-call, the development of these traits must here be influenced by both sides. While the influence from the *lar* side could have been managed through learning processes, the influence from the *pileatus* side, given the lack of an acoustical model, could only be explained through genetical processes.

The great-call of both gibbon females and the additional short phrase (coda) of the hybrid male are combined to a duet structure, typical of many gibbon species. A similar duet form identifies, for example, the great-call sequence of *H. lar*. Also here the male normally joins his own phrase to the song only after an individually specific interval occurring at the end of the great-call (fig. 4b). This behaviour appears quite different with the second parental species, *H. pileatus* (fig. 3b). Here, the male typically enters in the song with his phrase during the female's great-call [Brockelman, 1975; Geissmann, 1983; Haimoff, in press a; Haimoff et al., 1982; Marshall et al., 1972; Marshall and Marshall, 1976]. The finding that this hybrid male did not begin his phrase during the great-call, but rather waited a specific interval to begin, may be due to a characteristic inherited through the maternal side (that is, through *H. lar*), and which the male hybrid could not have taken over from his father.

Two other plausible interpretations for the same finding should be taken into consideration: With *H. pileatus* pairs, the male's entry into the female's great-call sequence could be released by the special structure of the female duet part. The trill, typical of *H. pileatus*, could be the reference point which he uses for his striking in. Since this trill is lacking with *H. lar* and with the hybrid female, there would be no corresponding reference point available, and therefore a male would not enter during the great-call of his partner.

However, recorded tapes from the Zoological Garden in Zürich speak against this interpretation. Here a *pileatus* male sings with several *lar* females, and enters with his part of the duet invariably during the great-call of the females. Tembrock [1962, 1964, and cit. in Schröpel, 1977] describes a similar duet from a gibbon pair in the Zoological Garden in Berlin (DDR). Here as well, the male began with his duet part during the great-call of the female. On the basis of the detailed description of phrase structure and note repertoire [Tembrock, 1962], the female can be identified as *H. lar*, the male, however, as *H. pileatus* (although catalogued as *H. lar* in the cited text). Apparently, *pileatus* males are able to maintain their species-specific pattern of song entrance in duets with *H. lar* females.

In this connection, it may be of interest to note that with a further gibbon species, the grey gibbon, *H. muelleri*, the great-call of the female contains a trill similar to that of *H. pileatus* [e.g. Marshall and Marshall, 1976]. But, in opposition to the latter, the male of *H. muelleri* does not respond during the great-call. This could be a further indication that the overlapping of male and female song parts in the great-call sequence of *H. pileatus* is not conditioned by the female's trill, respectively that the lacking overlap in the song of the hybrids and their mother had not been evoked by the absence of the trill. The male of *H. pileatus* and the hybrid male do not seem to depend on the trill of the female in the timing of their contribution to the great-call sequence.

There is a further possibility of interpreting the missing overlap of the male and female duet parts in the great-call sequence of the hybrids: The male could take the start of the great-call as a reference point, and after an individually specific interval enter in, regardless how long the entire great-call of the partner lasted, and how developed it is at the point of the male's entrance. An overlap of the song parts would then occur when the female's great-call lasted longer than the male's preferred entry interval, measured from the start of the great-call.

Since the great-calls of both females in the hybrid group lasted a shorter period (hybrid female: median = 12.0 s, mother of the hybrids: median = 14.3 s, see above) than that of an average *H. pileatus* great-call (median = 16.4 s), it would follow that the entry point of the male's phrase would no longer fall within the female's great-call. But neither can this hypothetical mechanism answer, or completely answer, for the varying duet structure between *H. pileatus* and that of the hybrids. In the duets, mentioned above, of a *pileatus* male with several *lar* females in the Zürich Zoo, the male's entry point would fall within the females' great-call, although at least 1 of these females also sang shorter great-calls (median = 13.7 s, range 12.5-13.8 s, n = 3) than typical *pileatus* females. If, therefore, the duct part of the hybrid male did not overlap with the great-call of the 2 females, it would appear that this behaviour does not or not exclusively depend on the structure of the great-calls. The behaviour could be much more dependent on the male himself. Since the hybrid male could not have learned from his *pileatus* father this duet pattern which is typical for *H. lar*, I infer that there is a genetic basis for this behavioural characteristic, too, which the hybrid male inherited from the maternal side.

Table II. Analyzed characteristics in the song of 2 gibbon hybrids (*H. pileatus* x *H. lar*) and comparison with corresponding characteristics in songs of the parental species

Hybrid sex	Song char. No.	Song characteristic	Agreement with parental species	Genetical component
Male	1	constant use of inhalation notes in the male phrases	pileatus	?
	2	note rhythm in the male phrases (index)	intermediate	?
	3	expiration note in the male motif ascending	lar	?
	4	mode of entry of the male in the great-call sequence	lar	+
	5	three part motif	new characteristic	+
Female	6	note structure of the great-call	pileatus	+
	7	acceleration of note succession in the great-call	pileatus	+
	8	note rhythm at the end of the great-call (climax)	intermediate	+
	9	overall note rhythm of the great-call (index)	intermediate	+
	10	number of notes in the great-call	intermediate	+

+ = Traits for which a genetical component could be shown.

The analysed song characteristics of the 2 gibbon hybrids are again presented in table II. Out of 5 characteristics from the organizing and the great-call sequence of the hybrid male, 2 are developed like those of *H. lar*, 1 is like *H. pileatus*, 1 is between both parental species, and with 1 characteristic, there is no apparent analogy to the parental species.

Out of 5 song characteristics from the hybrid female's great-call sequence, 2 are formed as they are with *H. pileatus*, and 3 are intermediate between the conditions of both parental species. For 7 of the 10 characteristics examined, an inheritable component can be shown. This genetic determination can be traced with 1 of the characteristics of the hybrid male from the mother's (*lar*) side, with all 5 traits of the hybrid female it can be traced from the father's (*pileatus*) side.

The hybrid singing behaviour examined here must not, of course, necessarily agree in all respects with the singing behaviour of other F1 hybrids. Nevertheless, the findings here presented show clearly that a previously postulated genetic determination of gibbon song characteristics (see 'Introduction') exists – at least for these hybrids. That learning plays an additional role, such as Fox [1977] and Miller [1971] supposed, cannot be precluded.

The traits which characterize the song of these hybrids are also to be found in other gibbon species; not necessarily, however, the parental species. What is new in particular is the combination of these traits. The similarities in singing behaviour found here between hybrids and those gibbon species not involved in this interspecific hybridization (*H. agilis*, *H. moloch*) can only be partly explained by a mosaic-like combination of song characteristics from the two parental species, *H. pileatus* and *H. lar*. The resemblances between the male hybrid's phrases and those of *H. agilis*, as well as the remarkable similarities between the great-call of the female hybrid and that of *H. moloch*, show that a closer relationship probably exists between these species and the parental species of the hybrids. By several authors, these species, together with a further one, *H. muelleri*, have been united, on the basis of mainly morphological characteristics, in a sub-grouping of the hylobatids (*H. lar* group), for which closer taxonomic relationships within the framework of the Hylobatidae was suggested [e.g. Creel and Preuschoft, 1976; Groves, 1970, 1972; Haimoff et al., 1982; Pocock, 1927].

Extended research comparing songs of gibbons with gibbon hybrids could, then, not only provide information about the transference mechanisms of song characteristics between generations, but also provide a basis for additional information concerning taxonomic relationships within the hylobatids.

Summary

The song of 2 gibbons in captivity, a male and a female hybrid (*H. pileatus* x *H. lar*), has been analysed. The species-specific song characteristics of neither parent species could be found in the hybrid song. The features which characterize the song of the hybrids generally also occur in other hylobatids (not necessarily the parental species). It is almost exclusively the combination of these features which seems to be new in the hybrid song. The song characteristics of both hybrids show influences from *H. pileatus* as well as from *H. lar*, and some characteristics are intermediate to those of each parental species. An at least partial genetical determination can be shown for 7 of the 10 analysed characteristics. Apart from similarities to the songs of the parental species, the song of the male hybrid resembles in certain characteristics that of *H. agilis*, and especially the ‘great-call’ of the female hybrid exhibits remarkable similarities to that of *H. moloch*. These similarities can be explained by the recombination of parental song characteristics, but also suggest a close relatedness of the four species already mentioned. The song of the male hybrid is further characterized by specific three-parted motifs which are not typical for neither parental species and which cannot be explained by simple combination of their song characteristics.

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