The Onset of Siamang, Hylobates (Symphalangus) syndactylus, Vocalizations in Captivity and the Role of the Exhibit Environment

By

Matthew Brewer

A paper submitted in partial fulfillment of the requirements for the
Bachelor of Arts in Anthropology
Department of Anthropology

The Colorado College

April 6, 1999

ON MY HONOR I HAVE NEITHER GIVEN NOR RECEIVED UNAUTHORIZED AID ON THIS PROJECT

_____

Acknowledgments

Thank you to the swinging singing Siamang of the various zoos for not throwing their feces at me, and being my exciting subjects.

Thank you to the many zoo keepers who helped me to learn about the exhibit environments and Siamang that inhabited them.

Thank you to Mike Nowak for reading through the multiple drafts and making sense of the nonsense.

Thank you to those who learn something by reading this paper in its entirety.

Dedication

This paper is dedicated to the swinging singing Siamang, whose infamous vocalizations always brightened my day with an urge to mimic and respond only to endure the laughter by them and the other zoo visitors.

Quotations

"New opinions are always suspected, and usually opposed, without any other reason because they are not already common."
(John Locke, Essay on the Human Understanding, cited in Cohen 1960:235)

"In every good zoo the animal does not feel itself in any way a prisoner, but — as in the wild — it feels more like a tenant or owner of a piece of land"
(Hediger 1969, cited in Shepherdson et.al. 1998:xvii).

"Example is the school of mankind, and they will learn at no other."
(Edmund Burke, Letter on a Regicide, cited in Cohen 1960:81)

"No arts, no letter; no society; and which is worst of all, continual fear and danger of violent death, and the life of man, solitary, poor, nasty, brutish, and short."
(Thomas Hobbes, Leviathan, cited in Cohen 1960:190)

"When you think more on the value of all you think less of the past and more on the preservation of the future."
(Dian Fossey, (paraphrase) Last Journal Entry)

"Words are of course the most powerful drug used by mankind."
(Ruyard Kipling, Speech 14 February, 1923, cited in Cohen 1960:225)

"He who *can* does, he who *cannot* teaches."
(George Bernard Shaw, Man and Superman, cited in Cohen 1960:358)

Table of Contents

List of Figures

List of Tables

Abstract

The onset of Siamang vocalization in captivity and the wild are for many of the same reasons. Vocalizations establish a territory, increase group cohesion, and create a buffer zone between territories. In captivity many factors, such as food availability and shelter, remain consistent and do not inhibit a necessity to vocalize; in fact, because of the increased idle time (resting, grooming, etc.) vocalizations occur more often in captivity. Furthermore, the exhibit environment plays a key role in establishing a territory by providing a naturesque ecosystem that emulates feral environments at the same time educating the public. This study, therefore, explores the role of the exhibit environment in four North American zoological gardens. A traditional, semi-traditonal, semi-stimulational, and stimulational exhibits are explained, as well as the extent that environmental stimulation and the weather contribute to vocalization onset. Results indicate that stimulational exhibits establish a defendable territory more readily than traditional exhibits.

I. Introduction

The modern zoological garden, as we know it, emerged in 1828 when the Zoological Society of London opened the doors to the Zoological Garden in Regent's Park. The zoo quickly encapsulated the rising middle class with education, the exotic, and mystery to become tremendously popular (Hancocks 1995). Early zoos housed animals in concrete floored buildings with bars and cages to separate them from the public and little or no environmental stimulus. Beginning in the 1970s zoos began to move away from concrete houses to open naturesque environments that emulate feral environments (CMZ 1998; Orgeldinger 1997; SFZ 1998; Shepherdson et.al 1998; WPZ 1999; ZSSD 1999). This change reflected both the animal well being and education of conservation research efforts (Conway 1995).

Primate ethnology studies provide a sound basis for the range of animal well-being needed to facilitate exhibit environments. In traditional exhibits, chimpanzees suffered from depression, baboons tore their hair out, and gorillas made fecal art (Goodall 1971). Primate cognition studies with American Sign Language (ASL) recognized the intelligence of the great apes (Blum 1994; Morgan 1995; Savage-Rumbaugh 1984); social behavioral studies among large troops of rhesus and macaques contributed to the importance of the environment to group well-being (De Waal 1989); environmental stresses that were otherwise taken for granted became paramount and forefront in establishing both a tourist site and animal well-being (Norton et.al. 1995).

Communication studies among Hylobatids — gibbons and Siamang — are just as important as ASL studies with Pongids — gorillas chimpanzees, and orangutans — to establish language variation among non-human primates. The fact that very little has been written about Siamang vocalization in captivity with relation to the exhibit environment provides the basis for this study. (zb1997; Geissman and Hulftegger 1994; Orgeldinger 1991, 1993, 1996, 1997).

The exhibit environment is the fundamental component of the zoological garden; it is both an ecological and general housing system. For the purpose of this study there are two types of exhibit environment: traditional and stimulational. The latter are best effort attempts to emulate the environment that the animal occupies in the wild. The former are simply concrete buildings with little or no ecological components; there may

be logs, from long dead trees or ropes and steel bars, but there is no live environmental stimulus. The increased the environmental stimulus, and more naturesque the exhibit, provides a zoological setting appeasing to both the public and the animal. The more naturesque exhibit functions to educate about both the animal and its ecosystem, which has a profound effect on wild conservation.

This study, therefore, seeks to determine the coupled effect of the exhibit environment with the onset of Siamang vocalization in captivity. For comparative purposes of general ecological and social behavior of feral populations monographs will be used (Chivers 1972, 1974; Gittins and Raemakers 1980; Prueschoft, et. al. 1984). Because many factors that induce environmental stress in the wild, such as food and shelter, are consistent in zoos there are two secondary factors that effect vocalization onset: environmental stimulation and the weather.

With this in mind, this study addresses both zoological critics and the zoological organizers. To the latter it supports the recent moves towards emulating outdoor feral environments to provide for the establishment of territories that can be actively defended as they would be in the wild. To the former, though it in no way condones the creation zoos in the first place, it advocates that traditional zoos be should pressured to update their exhibits for the well-being of the animal and better educate the public.

> By encouraging and supporting the pervasive use of environmental enrichment for captive animals, zoos, aquaria, and laboratories are providing opportunities for animals to have some control over the environments and to occupy their time with species-appropriate activities. By most measures developed and by most definitions used, environmental enrichment increases an animal's psychological well-being. We believe that animals whose lives are enriched represent true ambassadors for their species; in turn, their enhancement facilitates the role of zoos and aquaria as conservation educators (Mellen et.al 1998:334).

This study, therefore, considers the exhibit environment of four North American zoological gardens as they pertain to the onset of Siamang vocalization. Each exhibit, when put in the following order, builds upon the previous with additional environmental stimulus beginning with the traditional and progressing to the stimulational: Cheyenne Mountain Zoo (CMZ), Colorado Springs, Colorado; San Francisco Zoo (SFZ), California; San Diego Zoo (SDZ), California; and Woodland Park Zoo (WPZ), Seattle, Washington. (CMZ 1998; SFZ 1998; WPZ 1999; ZSSD 1999; See also section V).

II. Background

Classification and Phylogeny

The Siamang, and the gibbon, are members of the family *Hylobatidae*. The family *Hylobatidae* has often been categorized as the "lesser apes," simply because the overall size of the gibbon and the Siamang is much smaller than the "great apes" — the bonobo (*Pan paniscus*), the chimpanzee (*Pan troglodytes*), the gorilla (*Gorilla gorilla*), and the orangutan (*Pongo pygmaeus*). Hylobatids are brachiators, and several significant morphological changes have occurred to the thorax and shoulder, elbow, wrist joint, hand, trunk, and lower limbs that differentiate them from Pongids. The thorax is broader with a stout, S-shaped clavicle to allow firm attachment of the deltoid muscles, and the proximal epiphysis of the humerus is larger than the femur. The elbow joint offers great stability and power of extension (much more so than quadrupeds), with a greater extension velocity because the triceps muscle is closer to the joint fulcrum. The wrist joint displays a meniscus between the styloid and triquetral, which becomes ossified, and is known as *os daubentonii*; the same is often seen in humans. The hand is adapted into a suspensory hook. The brachiating posture, like the bipedal, orients the trunk more or less vertically. The lower limbs, which stabilize during arm suspension, exhibit great mobility (Groves 1972:3-5).

The Hylobatid phylogeny has long been problematic. The differentiation made between Pongids and Hylobatids are slight, especially when speaking of "the Siamang, the most great-ape-like-gibbon, and the pygmy chimpanzee, the most gibbon-like-great-ape" (Groves 1972:11). This view is shared by Schultz (1933:417) who concludes

> In a phylogenetic 'family tree' this would have to be represented by two generic branches diverging very little but reaching in the Siamang beyond the level attained by the gibbons. Both branches would have to be directed more or less parallel to a branch showing the evolutionary trend of the orang-utan. The latter branch would be approached a good deal more closely by the Siamang than by any of the gibbons.

Figure 1 is a reconstructed phylogeny, identifying symplesiomorph and synamorph characteristics of the Hylobatid family. The Siamang (2a) is not the most primitive (1a),

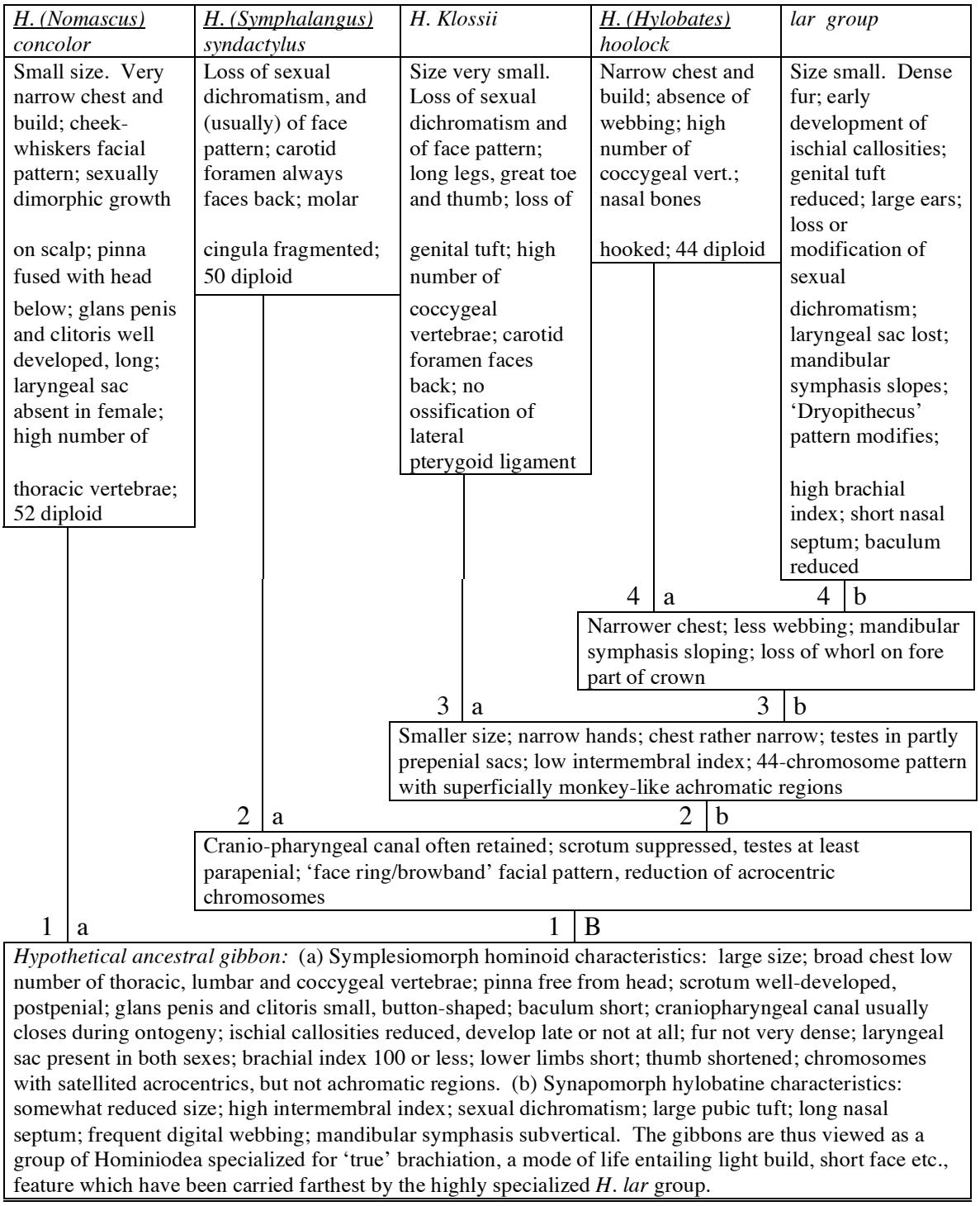

Figure 1: Reconstructed Phylogeny of the Hylobatidae (Adapted from Groves 1972:81).

but exhibits many symplesiomorph hominoid characteristics. Some (Kloss 1929, Richard 1985) argue that there is no significant difference between the gibbon and the Siamang and that the latter should be classified as *Hylobates snydactylus*. Others (Schultz 1933, Napier and Napier 1967, Chivers 1974) classify the Siamang in its own subgenus *Symphalangus* based upon the morphological differences outlined below. Groves (1972) classifies the family *Hylobatidae* into three subgenera: *Hylobates*, *Nomascus*, and *Symphalangus*. This classification (see Figure 1) differentiates the family further on the number of diploid chromosomes, and is classified as such: *Hylobates (Hylobates) lar* group — the white handed gibbon and others; *Hylobates (Nomascus) concolor* — the crested or Harlan's gibbon; and *Hylobates (Symphalangus) snydactylus* — the Siamang. The subgenus *Symphalangus* is represented by two species: the Sumatran Siamang (*H. (S.) s. snydactylus* Raffles 1821) and the Malayan Siamang (*H. (S.) s. continentis* Thomas 1908).

The Siamang differs from the gibbon morphologically by being larger and of a greater average weight (between 9 kg and 13 kg). Like the gibbon, however, sexual dimorphism does not occur. The coat is all black except for the area around the mouth and chin, which is grayer than the rest. The arms are longer in proportion to the legs than among gibbons. Both male and female Siamang have a laryngeal sac that inflates during vocalization to produce a monophasic boom (Napier and Napier 1967).

Ecological and Social Behavior

Siamang are restricted to feral locations on the island of Sumatra and the

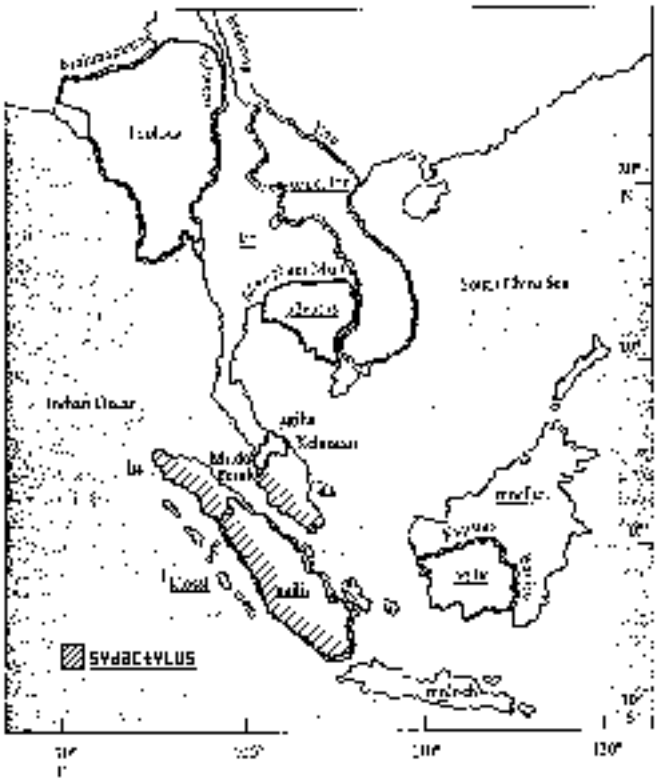

Figure 2: Distribution of nine gibbon species and the Siamang in Southeast Asia (Adapted from Richard 1985:332).

mainland peninsula of Malaya. Figure 2 displays both gibbons and Siamang throughout Southeast Asia. Figure 3 displays various Siamang and gibbon on the Malay peninsula. The topography (Figure 4) of the region is semi-mountainous — rising to roughly 7,000 feet above sea level. The climate is tropical receiving between 70 and 200 inches of rain yearly.

Figure 3: Distribution of gibbons and Siamang in the Malay Peninsula. J = Jerangau, Trengganu; M = Tanjong, Triang, Mersing, Johore; G = Ulu Gombak, Selangor; R = Ulu Sampan, Raub, Pahang; and T = Kuala Lombat, Temerloh, Pahang. ® = Siamang, o = white-handed gibbon, and Δ = black-handed gibbon (adapted from Chivers 1972:108).

In the rain shadow of the mountains it is drier, and therefore receives less rain. The annual temperature ranges between 65˚ F and 80˚ F. The flora zones into five climatic regions: lowland, hill, and upper dipterocrap forests transition "at about 1,000 and 2,500 ft. above sea level, respectively. Above 4,000 ft. are montane oak-forests, which are replaced at about 5,000 ft. by montane ericaceous forest" (Chivers 1974:7). Siamang are known to inhabit a range in the lowland, hill, and upper dipterocrap forests, between roughly 1,000 ft. to 4,000 ft. above sea level. The majority of rain (nearly 69%) falls between October and January. The remainder of the year receives roughly the same amount (greater than 80 inches) of rain in the remaining eight month period (Chivers 1972:110).

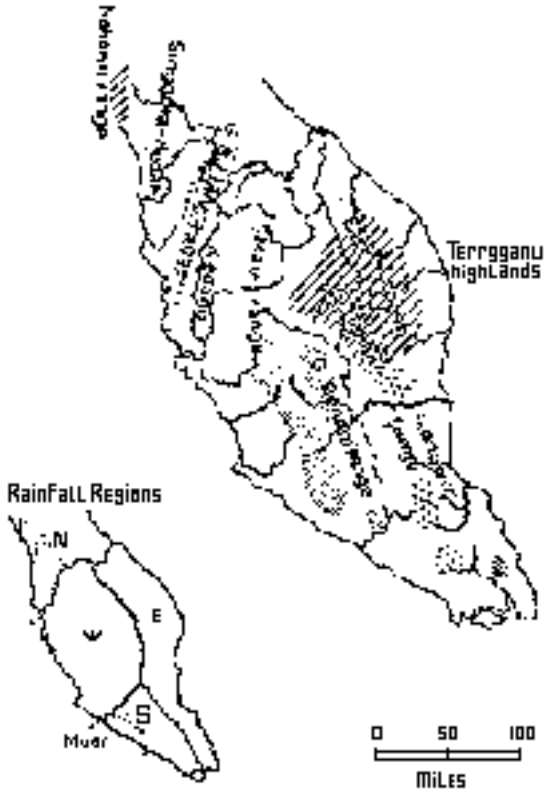

Figure 4: The Southern part of the Malay Peninsula, showing main rivers and mountain ranges, and contrasting rainfall regions (adapted from Chivers 1974:6).

The ranging behavior and territory of the Siamang is typically half that of the gibbon, whose biomass is half that of the Siamang. Day ranges are between 800 m and 1 km with a home range between 14 and 35 hectares (ha). The day range is defined as the total area traveled within the territory the group is known to occupy, and the home range is the overall territory occupied (Chivers 1974). Siamang usually take two to five days to travel trough the entire home range when food is abundant or readily available. "These long day ranges reflect a relative abundance of widely dispersed preferred fruits, whereas the shorter day ranges are associated with a more general abundance of lower-energy foods, i.e. leaf shoots, and so forth" (Chivers 1972:115).

A typical Siamang day begins at sunrise (about 0600h in feral locales) with a first feeding lasting until about 0900h. It is at this time that a vocalization bout is frequent. The group is usually active for 10.5 hours each day, settling in for the night between 1600h and 1800h dependent upon the weather. It is not uncommon for there to be a final feeding bout at or around 1800h on very active days.

The feeding habits of the Siamang are continuous throughout the day, including the time spent traveling between each feeding area. The diet consists of fruit, leaves (mature and immature leaves as well as stems and shoots), flowers and buds, and insects (caterpillars and crickets). Fruits range from small berries to large figs. Table 1 illustrates the overall proportions of each food type consumed. The majority of the diet is comprised of various leaves and fruits (predominated primarily by figs,

Table 1: Seasonal variations in food-type proportions at Kuala Lompat (adapted from Chivers 1974:78).

Food	'Season'							
	Intermediate, 49 days May—Aug. 1969		wet, 40 days Sept.—Dec. 1969		dry, 49 days Jan.—May 1970		total, 138 days	
	Visits/ Day	time/ day, min.	visits/ day	time/ day, min.	visits/ day	time/ day, min.	visits/ day	time/ day, min.
Fruits	2.6	84	3.8	125	5.9	132	4.1	111
Leaves, yg[1]	6.5	206	7.9	202	9.1	202	7.8	206
Flower, bd[2]	1.6	50	0.6	21	0.8	18	1.0	30
Insects	0.1	0	0.1	2	0.9	13	0.4	5
Figs	1.7	57	2.3	106	3.8	97	2.8	85
Total	10.7	346	12.1	355	16.7	365	13.3	354
	Visits/ Day, %	time/ day, %	visits/ day, %	time/ day, %	visits/ day, %	time/ day, %	visits/ day, %	time/ day, %
Fruit	24	25	33	34	35	36	31	32
Leaves, yg	61	61	64	59	54	56	59	58
Flower, bd	15	15	5	6	5	5	8	9
Insects	1	0	1	1	6	4	3	2
Figs	16	17	28	30	23	27	21	24
	Visit duration, min.		visit duration, min.		visit duration, min.		visit duration, min.	
Fruit	32.2		31.9		22.4		27.2	
Leaves, yg	31.9		26.8		22.2		27.2	
Flower, bd	32.1		33.8		21.5		29.5	
Insects	6.0		20.8		13.8		13.9	
Figs	33.1		46.4		25.2		30.8	
Total	31.6		29.5		21.8		26.6	

[1] Leaves, young
[2] Flowers, buds

amounting to nearly half of all fruit intake). Insects and flowers make up a small percentage of the overall diet. When drinking water Siamang rarely put their head into the water but instead gather water in and/or on their hand and lick it off. Further, Siamang are very selective in their diet, usually only eating those items that are blemish free. Siamang are classified as folivores with a preference for figs and some other fruit species, comprising less than 30% of the overall diet (Chivers 1972, 1974; Richard 1985).

The social organization of the Siamang is unique because they are monogamous. W.A. Mason (1968) explains that monogamous species are similar because they have no clear dominance among them, and are continually within close proximity of each other. He further notes the extent to which vocalizations play in maintaining group cohesion and the maintenance of territories. Not only are Siamang individuals rarely greater than ten meters from each other but also there is a paucity of intra-group communications. "Thus the high degree of coordination of members of a Siamang family group appears to be achieved by local enhancement resulting from subtle visual signals (rather than from conspicuous visual for vocal signals) and from habitual perception. By contrast more elaborate (ritualized) vocal and visual displays are involved in relations between groups" (Chivers 1976:133).

The average inter-individual distances while resting, feeding, and traveling, displayed in Table 2, also determine the average group size. A family unit, as it is often

Table 2: Mean distances between individual Siamang at Kuala Lompat during the wet and dry seasons during resting, feeding, and traveling (adapted from Chivers 1974:181).

Subject	Object						Mean distance
	M	F	SA	J	I	n	of other Siamang from subject, m
Rest							
Male		7.0	7.7	6.5	3.8	73	6.3
Female	3.3		4.7	5.2	3.2	54	4.1
Subadult	7.3	5.8		7.6	8.3	58	7.2
Juvenile	5.3	5.0	5.6		5.5	68	5.3
Infant	3.6	7.2	8.3	7.7		58	6.3
Total							6.9
Feed							
Male		7.5	9.8	8.1	4.9	219	7.6
Female	6.5		8.1	8.4	6.5	201	7.4
Subadult	10.4	9.2		10.3	9.7	231	9.9
Juvenile	7.5	8.1	9.7		7.1	210	8.1
Infant	6.7	6.2	10.8	7.6		183	7.8
Total							8.2
Travel							
Male		11.6	11.8	10.5	5.3	54	9.8
Female	12.1		13.6	10.0	11.1	54	11.7
Subadult	12.0	13.7		11.5	11.4	57	12.2
Juvenile	10.6	11.3	13.1		10.1	60	11.3
Infant	4.0	10.6	12.4	10.1		62	9.7
Total							10.8

called, consists of a monogamous pair of an adult male and female, a subadult of either sex, a juvenile of either sex, and an infant. The infant is cared for by both the father and the mother, but may actually be cared for more by the father. Chivers recognizes two

stages of infant maturation: infant-1 and infant-2. During the former, the first 12-16 months of life, the infant is dependent upon the female. During the latter stage the infant is cared for almost exclusively by the male until about the third year of life when it is independent in group activities. Typically during traveling between one feeding area and the next the adult female will lead and the infant will remain with the father in the center of the group. The subadult usually maintains itself along the periphery of the group, and when it reaches full maturity, at about age six, will leave the group on its own accord to search a mate (Chivers 1972, 1974; Richard 1985).

Social activities such as grooming, play and aggression account for small percentages of daily activities, but are nonetheless important. These activities are more frequent in a captive context, since not as much time is spent traveling to food sources. Grooming occurred after feeding bouts, in either the early morning or more frequently in the afternoon when the group is fatigued and/or satiated, and constitutes roughly thirty minutes per day. Aggression does not occur often in the family unit, only on average 1.5 attacks per day — usually directed at the subadult. Play among the group is more of a self-play activity. This is because, for the most part, individuals are more than two years apart, so while the group is resting the infant may engage in self-acrobatics. This includes "from hanging and swinging in one place to chasing around small circular pathways …[to the]… bite[ing], chew[ing], or manipulat[ing of] small twigs" (Chivers 1974:216). The time spent on play is longer and more frequent with greater food abundance (Chivers 1972).

III. Vocalizations

The laryngeal sac makes Siamang vocalizations unique among the primate order. In a calling bout, sounds can be heard several kilometers from the source. Chivers (1974:235) provides an "analysis of the patterns of calling by a sample of groups from each area. Particular attention is given to variations in the frequency, timing and structure of group calls, the time calling starts each day, and the proportion of the local population calling." In what follows, the role of vocalizations, the typology of a bout, and general feral observations, will be explained.

Siamang vocalizations have a distinct typology. I have identified seven different vocalizations — three intra-group calls, and four included in the loud vocalizations. These include the bark, resonation or boom, chirp, grunt, scream, whimper, and whut. The bark, or vocal, is a high-pitched noise that sounds like "bop" and is consistent throughout the intra-group bout. The resonation, or boom, is produced by filling the laryngeal sac and produces a guttural grunt until the entire oral and nasal airways are filled; it usually lasts from one to five seconds and beings an intra-group bout. the chirp, grunt, and whimper are all inter-group vocalizations, and are rare; the most common, the grunt, is rapid forcing of air form the laryngeal sac out through pursed lips, and usually results from submission. The scream is diphasic, performed by the male only, and varies with the individual. the whut is a high-pitched "oohht" type sound, performed by the female only, and begins slow and becomes more rapid and staccato.

G. Tembrock (1972) paralleling Mason's (1968) group cohesion hypothesis among monogamous pairs, identifies five parameters of Hylobatid vocalizations. First, the syntax, or structure, includes sounds within a physical and spatial-temporal framework. Typical sound sequences, or stanzas, can be joined in a series to make a song; "the stanzas are heterotypic, they consist of different sounds and posses a pattern *specific to the species*" (Tembrock 1972:179, emphasis in original). The syntax is shaped by the channel-coding, or frequency, information transmitted and the difference between noise and signals. The syntactic outlines the structural picture of the song; the logical progression of the stanzas to make the song.

Second, the semantic conveys information about the relationship of the individual to the environment in three prominent categories: identity (species, group, individual,

sex, age), status (alertness, motivation, emotional status, social status, behavior), and environmental (disturbances, enemies, food, other ecological factors). Individual variation is an important component (Tembrock 1972:193). Even though the syntax is consistent, each male Siamang has a distinct scream, which can be readily identified.

Third, the pragmatic, or functional, aspect is paramount in distance regulation in social contexts. P. Maler (1968) divided spatial dispersion into four categories: (1) increased distance; (2) maintaining distance; (3) decreased distance, and (4) retained closeness and continuity. Tembrock (1972:199) distinguishes between contact communication and telecommunication; "we speak of contact communication when the animals have physical contact with each other, we distinguish between close field (permanent transmission of information) and distant field (temporary transmission of information). In both cases the song is broadcast in multiple directions."

Finally, the metrical and sigmatic aspects are the least understood. The latter describes the relationship between the sign and significance, insofar as they become iconic symbols. The former convey a quantifiable amount of information; "the stanza songs of the gibbon and Siamang contain interesting production of algorithms for the stanza structure which can perhaps be analyzed with methods of generative grammar" (Tembrock 1972:202).

A typical calling bout contains three phases of vocalization. A bout is preceded by faint monophasic booms or resonations, and the laryngeal sac is filled at this time. Following the faint resonations are single barks and chatters that precede the regular series, usually in group cohesion. The regular series follows a 1—1-2-3, 1—1-2-3 pattern. In this pattern a single bark is followed by one to three short series of three to twelve barks each. At the height of the series the barks become more frequent and staccato-like. These barks are accompanied by diphasic resonations between the series. Calling bouts are initiated by male chatters or female grunts and the rhythmic whuts by females culminate into bark-chatters by all and screams by males at three minute intervals (Chivers 1974).

There exists a degree of sexual dimorphism within Siamang calling bouts. The male screams occur at one, two, or three minute intervals. The female barks, ranging between bouts of three to thirty consecutive barks, are generally forty-five seconds to two-and-a-half minutes apart. Table 3 illustrates male and female call characteristics in a sample feral population, and Table 5 (page 38) displays similar information in captivity.

Table 3: Siamang male and female call characteristics (adapted from Chivers 1974:263).

Group	Call duration	Male, average number of screams per minute	Female, average number of bark series	Average number of barks in each part of bark series		Mean interval between bark series, minute	
RS1	12.7	2.4	4.7[1]	18—6		2.7	
RS2	18.1	3.0[2]	6.3	12—7		2.9	
RS1B	17.0		5.9	14—7		2.9	
RS3	16.2		6.9	18—9		2.4	
RS4	22.0		7.8	14—7		2.8	
RS4A	13.5		6.2	15—9		2.2	
RS11	23.3	3.3	6.9	13—7		3.4	
RS12A	21.0	3.6[2]	5.6	15—7		3.8	
RS12	15.2	2.5	6.6	15—8		2.3	
Ulu Sampan	17.6	3.0	6.2	15—8	581[3]	2.8	128[3]
TS1	10.2	3.7[2]	4.6	15—7		2.2	
TS5	14.6		5.9	20—7		2.5	
TS4	13.3		5.8	19—9		2.3	
TS6	10.0		4.8	21—8		2.1	
Kuala Lompat	12.1	3.7	5.2	16—7	277[3]	2.3	76[3]
GS6	17.8	3.8	8.0	18—8		2.2	
GS16B	14.1	3.0	4.8	17—6		2.9	
GS16C	14.0		5.3	15—7		2.6	
Ulu Gombak	15	3.4	5.7	17—7	83[3]	2.6	16[3]
Total	15.5	3.1	5.8	15.5—7.5		2.7	

[1] Two females call in group (one subadult).
[2] Two males in group (one subadult).
[3] Sample size

Inter-group conflicts among the Siamang are rare, and vocalizations play a key role in maintaining group cohesion. Chivers (1974) observed no increase in intensity of female bark or male scream in inter-group confrontations. Chivers (1976:130) differentiates three levels of interaction: "(1) asynchronous (sequential) group calls, not necessarily directed at a neighboring group; (2) simultaneous group calls, usually across the territorial boundary; and (3) males chasing each other to and fro across the boundary." Moreover, the inter-group vocal bouts serve, in addition to increasing group cohesion, to establish a buffer zone between territories (Chivers 1976:131).

An alarm vocalization "was composed mainly of booms, barks, and bark-chatters, which lacked the continuity of group calls in spacing and defense situations" (Chivers 1974:242). These types of calls account for calls made after midday and during hours of darkness; calling bouts after midday are rare.

Calling bouts frequently start between 0700h and 1100h in captive and feral populations, but can be heard as late as 1200h. Table 4 shows onset time in various weather conditions between feral gibbons and Siamang. "Calling in both species started nearly an hour earlier on hot, sunny days … [and] calling [began] only twenty minutes later on cloudy and wet days" (Chivers 1974:263). There are seasonal variations in

calling bouts — increased in the wet season and decreased in the dry season — but there does not appear to be daily changes with relation to the weather other than time of onset. The seasonal variation was related to increased food availability in good weather at the start of the rainy season. The calls were inhibited by the rains throughout the remainder of the rainy season, and was continued into the dry season.

Table 4: Calling characteristics of gibbon and Siamang under different weather conditions, and seasonal variation in calling. **R** = observation site at Ulu Sampan; **T** - observation site at Kuala Lompat (adapted from Chivers 1974:263).

		Hot, sunny		Cloudy, wet	
		Siamang	gibbon	Siamang	gibbon
Onset Time	R	0827	0646	0847	0649
	T	0751	0712	0904	0758
Daily Proportion	R	0.19	0.30	0.21	0.31
of Population	T	0.32	0.44	0.26	0.40
Total		0.26	0.37	0.24	0.36
Call hours per day	R	3.1	4.2	3.0	4.4
	T	3.3	3.7	2.6	3.5
Total		3.2	3.9	2.8	4.0
Number of Days	R	14		24	
	T	21		17	
Total		35		43	

	Siamang		Gibbon	
	Ulu Sampan	Kuala Lompat	Ulu Sampan	Kuala Lompat
Number of Group Calls/day				
January—April 1969	2.57	2.13	3.86	4.15
May—August 1969	2.22	3.00	4.34	6.62
September—December 1969	3.60	2.90	5.68	4.91
January—May 1970	1.91	3.77	3.00	4.46
Number of Days	165	203	165	203
Total	2.54	1.94	4.18	4.52
Number of Groups	11	9	9	9
Number of calls/day/group	0.23	0.22	0.46	0.57

The function of vocalizations in captive and feral populations are sometimes difficult to determine, as well as the cause of the bout. Chivers (1974:265) identifies three parameters of causation: "(1) group cohesion, specifically expressed in alarm and transformed into aggression; (2) dispersion, by advertisement of the group territory, and (3) territorial defense." Day-to-day fluctuations can also be explained among Siamang as one or more of the following: "(1) food availability enhancing individual energy intake to surplus levels; (2) reproductive behavior, with increased calling in consorting pairs and unmated individuals and (3) territory adjustments, resulting from disturbance[s], such as logging" (Chivers 1974:266). Therefore, well established pairs may vocalize less than a

newer pair (Chivers 1976). The most important role of vocalization is inter-group maintenance and establishing group cohesion.

Vocalizations in captivity serve the same purpose as feral populations, however, most captive Siamang do not have visual or acoustical contact with other Siamang. Orgeldinger (1996:34ff) posits three questions about the nature of captive vocalizations: "(1) Is there any difference in territorial behavior of wild and captive Siamang and what part do human rivals take in the zoo? (2) Are there any sex differences in maintaining the territory? (3) Can we find a difference in territorial behavior in captive pairs with or without contact to neighboring conspecifics?"

The exhibit environments serves as a reduced home range and regards human visitors as rivals, therefore, the comparison of protective and territorial behavior in captive and feral Siamang differentiates the vocalization role. Orgeldinger (1997:319) explains that "protective and territorial behavior are hard to distinguish under zoo conditions and furthermore humans are regarded as rivals." Indeed, Siamang with neighboring conspecifics spend more time duetting than groups without such neighbors, and always sing together (1997:322).

The mean percentage of daily activities spent vocalizing is higher in captivity than in the wild. Orgeldinger (1997) cites a mean of 4.7% and 1% in captivity and in the wild, respectively (see section VI, page 38). The major difference "seems to be the higher amount of disturbances in the zoo. Furthermore, "human rivals and neighboring conspecifics are responsible for this increase in Siamang" (1997:319). The male Siamang is more perceptive to everything occurring outside the exhibit (e.g. unknown noises, visitors, zoo staff, other animals, and conspecifics) than the female and is more likely to react (1997:321).

Therefore the role of captive vocalization, as concluded by Orgeldinger (1997:323) warrants a continual need to defend the reduced territory, and in some cases even more so than in the wild.

1. The quality of protective and territorial behaviors is similar in wild and captive Siamang. In captivity, the territorial response to human and conspecific rivals is similar.
2. Males are more active in nonvocal territorial behavior than are females, and they could be found more often in the front part of their enclosures. Males are more attentive to events outside the enclosure than their mates, whereas females concentrate their attentiveness on special persons or females of a conspecific group.
3. Although the length of songs and the temporal distribution of calling throughout the day are equal or similar in the wild and in the zoo, the

duetting rate is much higher in captivity. Furthermore, Siamang having acoustic and visual contact with neighboring conspecifics spend more time in singing than do Siamang without such a neighbor.

4. In captivity, pairs without young seem to be more engaged in protective and territorial behavior than parents. This might be because they have more free time (Orgeldinger 1997:323).

Sporadic alarm to noisy school groups, a large, obnoxious individual, or a well-known regular may cause increased vocalizations. The presence of conspecifics, or sympatric species (e.g. gibbons), and other Siamang groups, may also increase vocalization occurrences.

IV. Data, Methodology, and Observations

Observations followed two methods: *ad libitum* observations and individual focal follows (IRFs). Figures 5 and 6 are examples of ad-lib observations and IRFs, respectively. Ad-lib observations allow one to observe all individuals at the same time by noting what they are doing at any given time, and to record thoughts and other pertinent observations about patterns and styles. Ad-libs also allow the observer to reflect critically on what has already been observed.

IRFs follow an individual over the course of fifteen minutes and records behavioral contexts and behaviors at one minute intervals. IRFs help to determine percentages of daily maintenance activities such as feeding, resting (grooming and idle time), locomotion, play, and vocalization. IRFs record five observable characteristics: context, behavior, on/off ground, proximity, and location, as well as additional comments. The on/off ground category records the position of the focal animal in relation to the vertical horizon. The proximity includes three degrees: touchable (1), reachable (2), and same cage (3), and sometimes a fourth degree — other cage (4) — when the animal is not observable. The location within the cage is noted at each observation. All context and behavior codes consist of four letter codes. The IRF was originally used in conjunction with computer programming and the Chimpanzoo project put forth by Jane Goodall at CMZ. There are six context codes used exclusively in this paper, one is exclusive to Siamang and was not an original context (Philippart 1991), and forty behavior codes. An explanation of each context and behavior codes are explained in Appendix II:

Observations at CMZ were made for eighteen days between January 28, 1997 and February 28, 1997. All observations were done in the morning, typically from 0900h to 1130h. Two afternoon observations were made, one from 1400h to 1630h and another from 1345h to 1500h. A total of 2303 minutes of observations were done. A total of 240 minutes of IRFs were done on both Johore and Ungka, or 17 each. The weather was sunny and clear on three days, and partly cloudy on seven days. It was cloudy eight days, and it snowed three of those days (Brewer 1997).

Observations at SFZ were made for twelve days between September 25, 1998 and October 6, 1998. All observations were made between 1000h and 1300h, but I usually arrived at the zoo between 0830h and 1000h before it officially opened. A total of 1801 minutes of observations were done. A total of 375 minutes of IRFs were done on both Boy and Diabla, or 25 each. The weather was cloudy on six days, sunny on six days, and it rained on three days.

Observations at SDZ were made for twelve days between October 8, 1998 and October 19, 1998. All observations were made between 0900 and 1230h, but I usually arrived at the zoo between 0800h and 0900h before it officially opened. A total of 1827 minutes of observations were done. A total of 375 minutes of IRFs were done on Eloise and Unkie, or 25 each. The weather was sunny on six days, cloudy on six days, and it rained one day.

Observations at WPZ were made for ten days between June 6, 1998 and June 18, 1998. All observations were made between 0845 and 1230, even though the zoo did not officially open until 0930h. A total of 1804 minutes of observation were done. A total of 330 minutes of IRFs were done on Simon and Sutera, or 22 each. The weather was sunny one day, cloudy nine days, and it rained four days.

Figure 5: Example of an Ad-lib Observation.

31/1/97 @0912h S 60˚ FCMZ
should do time follow, not been fed yet.
@9:23 vocalize, gibbons started earlier (@9:20), seems to be in response to that; territory?
majority of vocalizing is resonance, followed by high-pitched bark, typically last 30s
begin to resonate in response to female gibbon call;
usually sit down while vocalizing; only one is vocal @same time;
begin to resonate than bark.
@9:33 female gibbon great call; both are idle no response to gibbons.
idle resting on ropes and logs, watching me.
Johore looking @food basket, searching for food.
@9:37 mangabeys or lemurs explode in short vocl session, Siamang appears frazzled but unmoved — no reaction.
@9:38 15 min. after 1st vocl, all has been quiet 5 min.;
Ungka pulled Johore off rope perch while walking underneath log.
@9:46 gibbon great call, no response by either female; little kid passed by, took no interest.
@9:48 fed, immediately began to eat;
Johore eats cucumber, green pepper; Ungka eats cabbage, green pepper; both very selective.
@9:51 gibbon great call, no response, eating.
went to pick up monkey chow that was thrown on the floor, and immediately they followed me while eating;
smells like dog food, very fibrous, uninteresting and bland compared to lettuce.
10:00—10:15 IRF; making noise with my clipboard, very intent on my actions; watching while grooming (Johore), coughed, looked @me (now Ungka gave me a short stare).
@10:17 wrestling, mild rough/tumble ==> grooming session.
@10:20 advance/withdraw, chase around exhibit;
whistled (yo), Johore looked @me intently, confused then ignored me.
@10:50 door opened by people, looked @me. make better drawing of cage (figure 7b).
@11:00 no response to still calling gibbon, swing and mild displacement — grunts and mouth wide (threat?)
@11:03 after 5 min. of gibbon vocl one grunt by Johore, after male began short solo; more grunts by Ungka.
@11:05 multiple grunts by Ungka during play.
@11:08 gibbon stopped, Johore and Ungka both on BS.
11:15 me voy ya!

INDIVIDUAL FOCAL FOLLOW FORM (IRFs)
(Adapted from AN306 and Jane Goodall Chimpanzoo Project)

Observations (obs.): 15 total at specified intervals (1 min.)
Contexts: AFFI, AGGR, PUOR, SONS, SIOR, SUBM
Behavior(s): see Appendix I for complete list
Proximity: 1-touching, 2-reachable, 3-same cage, 4-other cage
Vertical Location (in relation to ground — vrt.): on/off
Location: see appropriate figure of exhibit of individual of IRF (see figure 9b and 10b.1)
Comments: additional clarification of previous entries

Time 1033

Focal Unkie (SDZ) Date 10/14/98 #2 Weather 65° MC

obs.	Contexts	Behaviors	Vrt.	Proximity	Location	Comments
1	SONS	VOCL	off	2	@B9	resn, scrm :49
2	SONS	VOCL	"	3	@15a	hang, resn, vocl
3	SONS	RESN	"	2	@B14b	vocl, scrm :12
4	SONS	VOCL	"	3	@15	swng, brac, scrm :39
5	SONS	RESN	"	3	@15c	hang, vocl
6	SONS	SCRM	"	2	@B10	brac to @15a
7	SONS	HANG	"	3	@15a	vocl, resn, brac, scrm :25
8	SONS	VOCL	"	3	@15	hang, brac
9	SIOR	VOCL	"	3	@B	resn, scrm :13
10	SONS	SITT	"	3	@15c	resn, vocl
11	SONS	RESN	"	2	@15	sitt, scrm :20
12	SONS	VOCL	"	3	@14b	swng, brac, scrm :50
13	SONS	VOCL	"	3	@10	Brac
14	SONS	RESN	"	3	@Ab	vocl, sitt, scrm :38
15	SONS	HANG	"	3	@B14c/b	resn, vocl

Time 1111

Focal Simon (WPZ) Date 6/1098 #2 Weather 60° C (rain)

obs.	Contexts	Behaviors	Vrt.	Proximity	Location	Comments
1	SONS	FORG	on	2	@a	Forg straw next to sutera
2	SONS	FODH/M	"	"	"	", wtch me observe, eat spinach
3	SONS	FODH/M	"	"	"	Forg, eat carrot, straw
4	PUOR	FODH/M	"	"	"	Wtch people, forg, eat
5	PUOR	FODH/M	"	"	"	Eat lettuce, look at sut w/ straw
6	SONS	FORG	"	"	"	Eating, forg straw, wtch people
7	PUOR	FODH/M	"	"	"	"
8	SONS	FODH/M	"	"	"	", one arm on branch, sit ground
9	PUOR	WTCH	"	3	"	Wtch me take IRF
10	SIOR	WTCH	"	"	"	Wtch sutera, eat lettuce
11	PUOR	FODH/M	"	"	"	Wtch people and eat
12	SONS	FODH/M	"	"	"	Intermidst wtch, eat cabbage
13	PUOR	FODH/M	"	"	"	", cabbage
14	PUOR	FODH/M	"	"	"	"
15	PUOR	WTCH	"	"	"	Wtch me and people

Figure 6: Example IRF

V. Exhibits

The exhibit environments selected for this study include four zoological gardens at various stages of the traditional to stimulational spectrum. The most important criteria is the presence and use of vegetation, especially live plants. The exhibit environment with live vegetation provides more stimulus to actively defend than one with concrete and dead, placed logs. The letters, characters, and numbers in the following descriptions refer to locations used in IRFs.

Cheyenne Mountain Zoo

CMZ is a traditional exhibit environment with no vegetation. Enrichment vegetation, such as tree branches and boughs are sometimes present. The CMZ Siamang exhibit is

Figure 7a: CMZ Map.

presently inside the old feline house because the monkey house was emptied and eradicated with the completion of the Asian Highlands exhibit in late 1996. This new monkey house is an oval building with two entrances on the north and south sides. There are eight exhibits inside and three exhibits outside. The Siamang at CMZ are located on

the north end of the monkey house next to the entrance. If they are allowed outside, they are put into the adjacent enclosure outside the entrance (just beyond the north entrance towards the south). The service area is located, like an island, in the middle of the building. The access to the service area is between the fourth and fifth exhibits on the west side of the building. There is a third entrance directly across from the service area access. Figure 7a is a map of the zoo.

The Siamang enclosure is pentagonal in shape. Figure 7b details the identification system used in the IRFs explained above. Each branch has a specific number going from left to right, front to back, ground to ceiling. The letters "BS" refer to the back shelf along the back wall, and "BD" represents the service area access for zoo personnel. The food baskets are labeled "A" and "B", left and right, respectively. The ground is divided by a low rock and cement wall as foreground (F) and ground (G). The area toward the back wall, along the service area, is designated as the foreground, and between the wall and the front, the ground. The areas represented by the symbols "*" and "#" are the

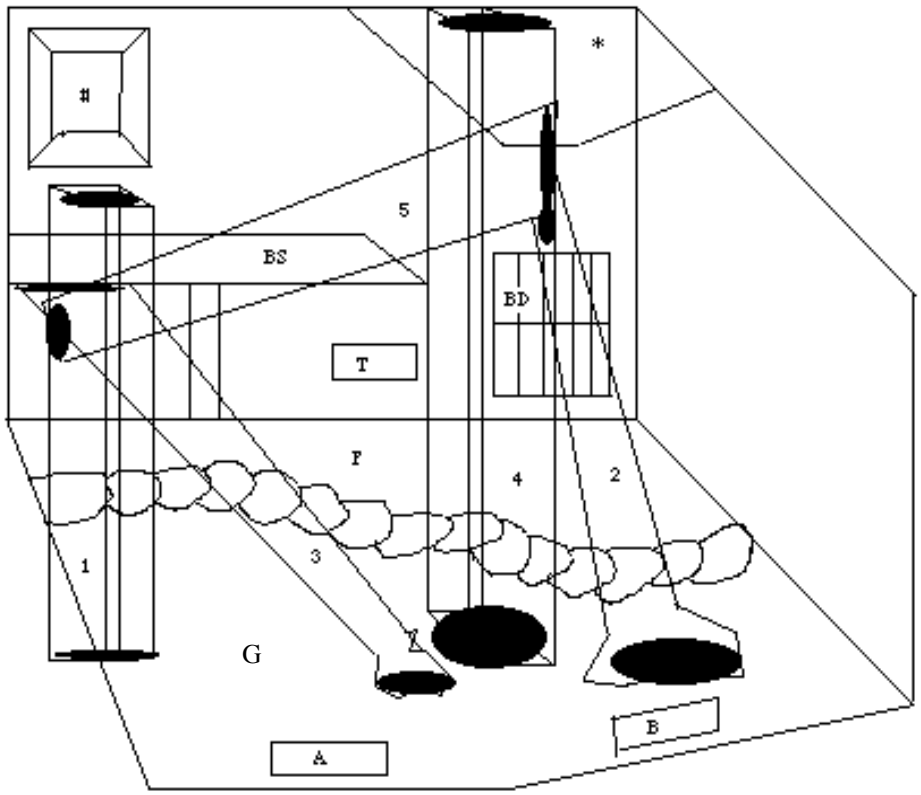

Figure 7b: Drawing CMZ Exhibit (See Appendix I.A for key).

ceiling and the access door to the Siamang holding area, respectively. The letter "T" represents the drinking fountain. in the enclosure. There are several ropes throughout the cage, labeled by their location relative to the branches and the back wall. The exhibit is roughly twenty feet wide (east/west) by thirty-five feet long (north/south) and fifteen feet

Figure 7c.1: Indoor Exhibit at CMZ

Figure 7c.2: Outdoor Exhibit at CMZ

tall. The building has a controlled temperature of 65˚ F, but is sometimes cooler if the doors are left open (Colahan 1997, personal communication). Figure 7c is a photo of the inside and outside enclosure.

There are two females present in the CMZ exhibit (Figure 7d). Their names are Johore and Ungka. The two have been together since mid 1996 when Joe, an older male, died and Juice, Johore's older sister, was relocated to River Banks, SC. A fifth Siamang, Caesar, died about the same time as Joe. Both were near expected life expectancy of twenty years or so, although some have been reported to live thirty years (Philippart 1991; Miller 1992).

Figure 7d: Photo of Johore (right) and Ungka (left). (adapted from CMZ web site <http://208.210.105.5:8081/newzoo/picutre.htm>).

Feeding occurs daily between 0930h and 1030h and again between 1430h and 1530h. In the afternoon various fruits are given, such as bananas, carrots. and oranges. In the morning the Siamang are fed various vegetables, such as cucumber, cabbage, kale, spinach, and green pepper along with monkey chow.

Johore was born the 22 of August, 1991. Her parents Joe and Gladys, another female and mate of Joe. Gladys died around late 1991. Johore is the larger of the two. She is best distinguished by her "wings" — tufts of hair above the ears. She can also be distinguished by her eating style. She will stand with one leg on the ground and hang with the opposite arm on the cage and forage and eat with the other arm, while her other leg is on the cage just above the food basket.

Ungka was born the 28 of March, 1991. Her parents were Rodney and Maggie, a monogamous pair that died soon after her birth. Because of this she was hand-raised. She does not have the wings that Johore does, and is smaller. The best distinguishing feature is the sucking of the thumb; a habit from being hand-raised. Her eating style is also unique; she puts both feet just above the basket and hangs with either the left or right arm (dependent upon which side of the basket she is on) and forages and eats with the opposite arm. During a calling bout Ungka's barks are more high-pitched than Johore.

Both Johore and Ungka are nearly six years old, classified as subadults. Siamang usually reach maturity at eight years old. There is no search to find either a mate since CMZ lacks both the space and is no need to breed Siamang (Colahan 1997, personal communication).

San Francisco Zoo

SFZ is a semi-traditional exhibit environment with external vegetation (planted along the periphery of the exhibit). At SFZ there are two Siamang exhibits, separated by several smaller exhibits, on opposite ends of a building (Figure 8a). Both exhibits, designated

Figure 8a: Map of SFZ (SFZ Website 1998)

East and West, are concrete floored surrounded by steel cages. The West Exhibit (Figure 8b) divides into six units, 'A' through 'C' (left to right) in the front and 'D' through 'F' in the back. The exhibit is roughly twenty feet long by twelve feet deep (from the front) and ten feet tall. Vegetation surrounds the north and west sides, but is set back from reach, and the east side connects to the building with an access door '®' and keeper access '*'. Two food bins are located on the south wall in units B and C. Several ropes crisscross the exhibit (G and H), while others hang from the middle bar (w, x, y, and z). A few logs (3 and 4) in the middle, between units B, E, F, and C connect to a shelf '#' above the access door. A hammock '2' provides a restful place off the ground. Figure 8c is a photo of the exhibit.

There are a total of five individuals at the two exhibits. Exhibit East consists of a mother, Mama East, and her daughter, Sia. Mama East was wild born in November of 1961. Sia was born October 15, 1990 (Pfirrmann 1998, personal communication). The

East exhibit was not observed because of time constraint and the presence of the male in exhibit West (since the pair-bond is more cohesive when it is male and female).

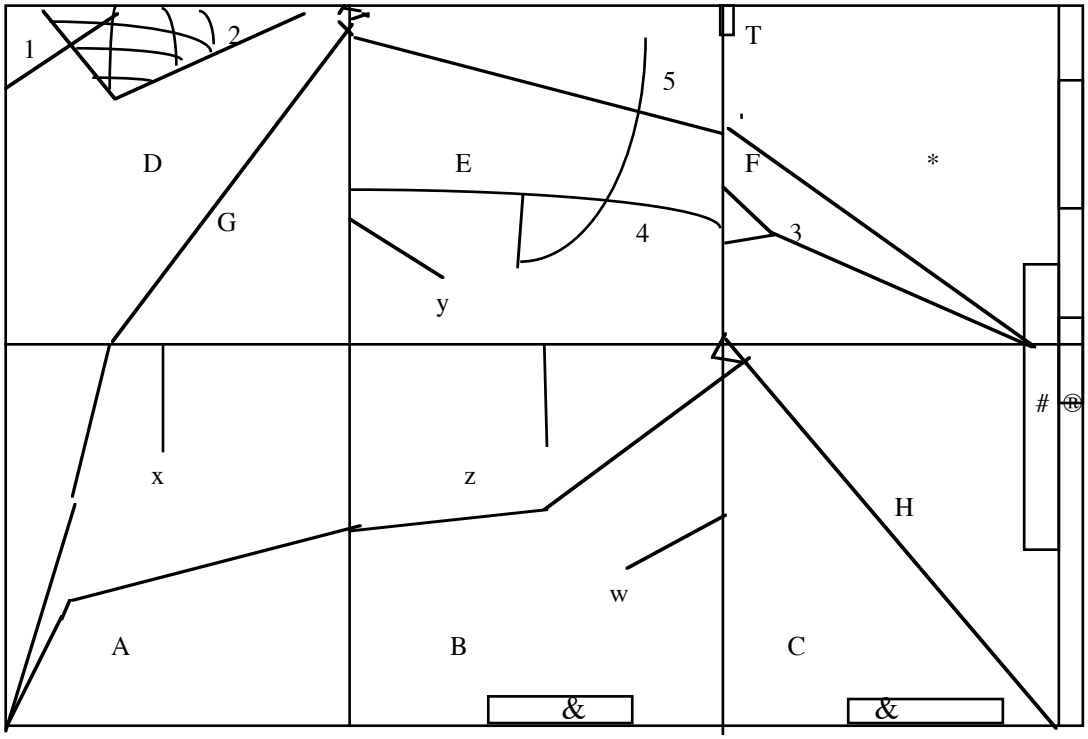

Figure 8b: Drawing of SFZ exhibit (See Appendix I.B for key)

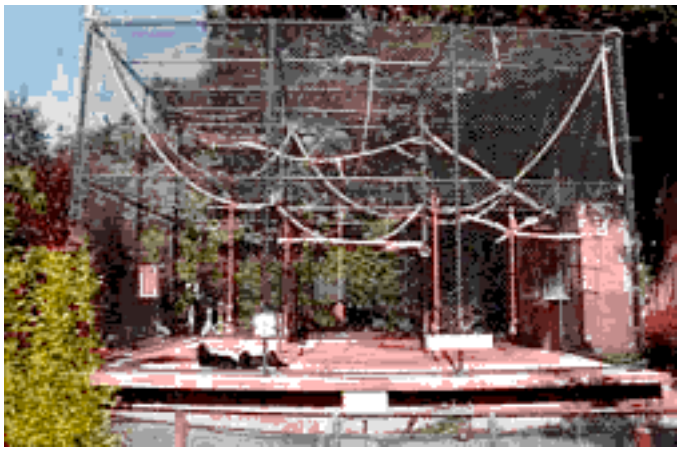

Figure 8c: SFZ exhibit

Exhibit West consists of a mother, Mama West, and her offspring, Boy (male) and Diabla (female). In exhibit West there is a male baby of Boy and Diabla, Storm,

born February 9, 1998. Mama West was wild born September 13, 1977. Boy was born April 8, 1992, and Diabla was born December 11, 1989 (Pfirrmann 1998, personal communication). Observations focused on the pair, Boy and Diabla, and ignored Mama West and Storm in IRFs. Figure 8d is a photo of Boy and Diabla.

Figure 8d: Diabla (left) and Boy (right) at SFZ

San Diego Zoo

SDZ is a semi-stimulational exhibit environment with live vegetation at the base of constructed "trees." SDZ (Figure 9a) displays "Siamang Island," with concrete shaped

Figure 9a: Map SDZ.

rocks, low-lying vegetation at the base of a wood and steel arboreal structure, and completely surrounded by water. The island (Figure 9b) is roughly eighteen feet (north to south) by thirty feet (east to west) and forty feet high at the tallest point from the water.

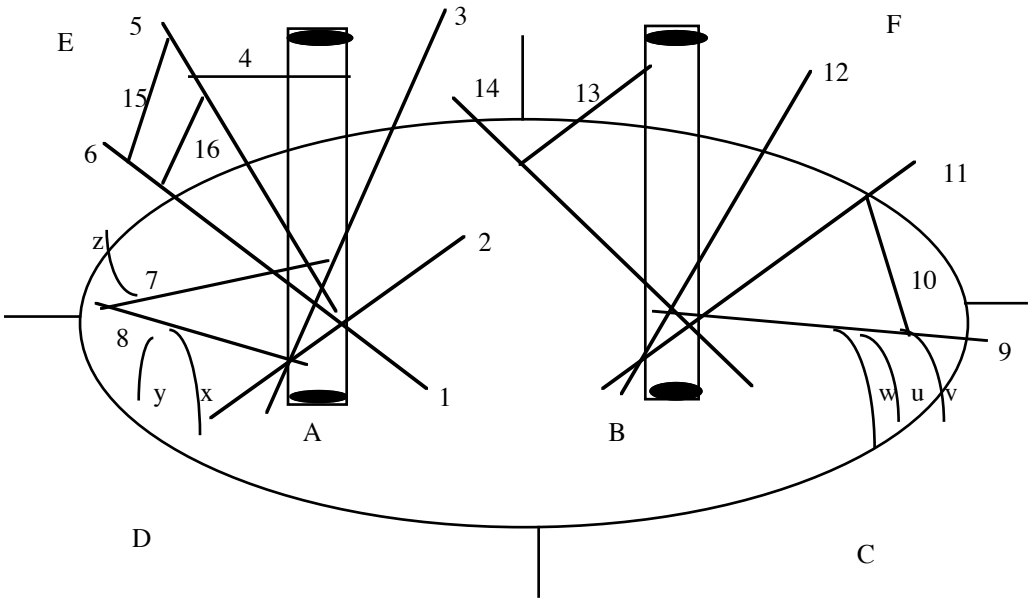

Figure 9b: Drawing SDZ Exhibit (See Appendix I.C for key)

There are two large adjacent upright poles (A and B), with both logs and steel bars rotated around like a tree. Each "branch" is numbered such that 1 through 8 and 15 and 16 are on A while 9 through 14 are on B. Projected at various angles from the numbered branches are steel bars labeled 'a' through 'f' as they correspond to the adjacent number (see Figure 6). The lower base, designated as the ground surrounding A and B and the outlying vegetation, divided into quadrants: C, D, E, and F, clockwise from the northwest corner. Various ropes (x, y, and z off A and w, u, and v off B) allow access from twenty feet in height to the ground. Figure 9c is a photo of the exhibit.

Feeding occurs daily between 1000h an 1100h, and includes various vegetables such as celery, onions, fig leaves, spinach, and eggplant. Various fruits, such as bananas, carrots, and apples, as well as monkey chow are put onto the island for stimulation and into the bedroom below (Bates 1998, personal communication).

There are three individuals at SDZ, a monogamous pair and their daughter. The adult male, Unkie, was born October 18, 1983. The adult female, Eloise, was born April 17, 1981. The daughter, Bagus, was born July 26, 1993 (Bates 1998, personal communication). Observations focused on the pair, Unkie and Eloise, and ignored Bagus. Figure 9d is a photo of Unkie and Eloise.

Figure 9c: Photo of exhibit at SDZ.

Figure 9d: Photo of Eloise (right), Unkie (center), and Bagus (left).

Woodland Park Zoo

WPZ is a stimulational exhibit environment with live vegetation in the outdoor exhibit; a large maple tree (about forty to fifty feet tall) stands in the middle and various other trees are planted at its base. The inside exhibit is mostly concrete shaped to emulate trees and rocks, but the ground is often covered by hay and other plants. When fed, the food is placed throughout the exhibit to encourage foraging. Figure 10a is a map of the zoo.

Figure 10a: Map of WPZ, with Tropical Asia Enlarged (adapted from Crowley 1995:63).

The diet consists of apples, banana, orange, grapes, carrots, yams, lettuce, kale, spinach, celery, broccoli, cabbage, and monkey chow. Outside enrichment foods include pine cones stuffed with pumpkin or sunflower seeds and bamboo stalks stuffed with pineapple or peanut butter. Feeding usually occurs daily between 0900h and 1030h (Shewman 1998, personal communication).

The inside exhibit divides into two parts, I and II, separated by a concrete support. I, on the south side, includes windows ‘a’ and ‘b’ , and ‘¡!’ (a seat in high branches occupied occasionally) and ‘®’ (another high point that acts as a seat). The drinking fountain, ‘T’ is in the back adjacent to the door to the outdoor exhibit. II, on the north side, includes windows ‘c’ and ‘d,’ and access to sequestered bedrooms below. Access

for the keepers, '&,' is on the south wall of side II. Above the entrance to the bedrooms is a hammock and various plants. The exhibit is about fifty feet long (north/south) by eleven feet wide (east/west) and ten feet tall. The inside exhibit has a controlled temperature of 65˚ F, sometimes a little less when the access to the outside is left open (Shewman 1998, personal communication).

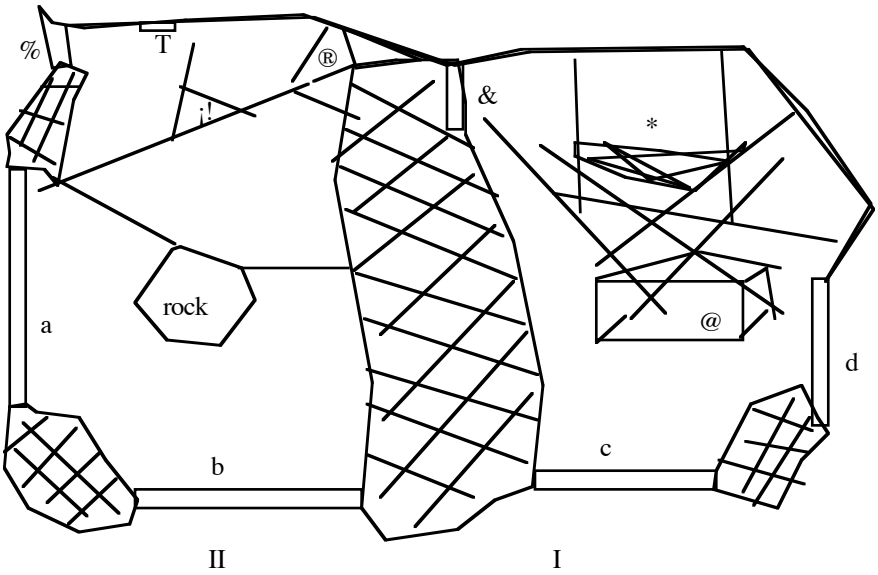

Figure 10b.1: Drawing WPZ indoor exhibit (See Appendix I.D for key)

The outside exhibit is a semi-circular island, surrounded by water on all sides

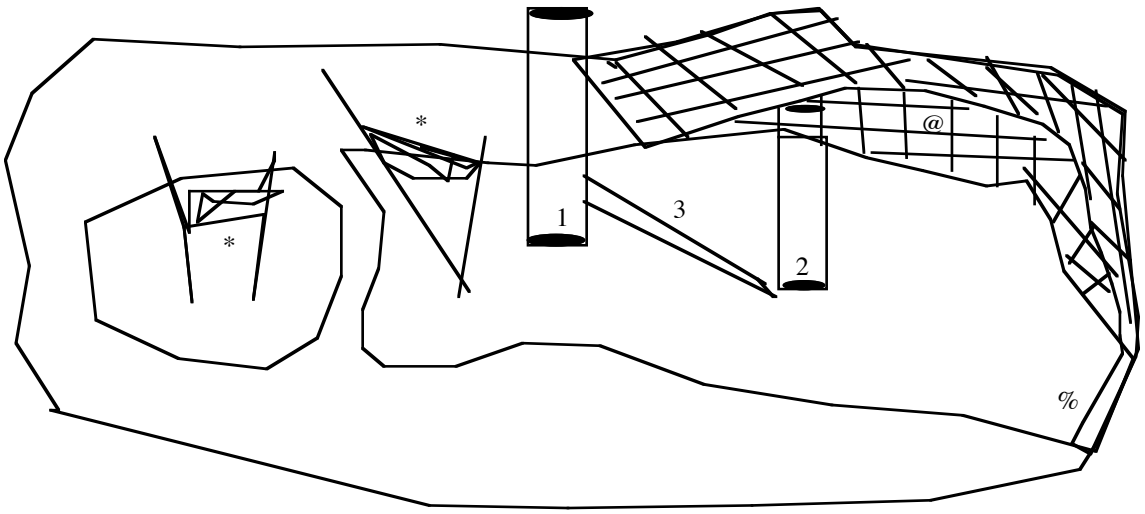

Figure 10b.2: Drawing WPZ outdoor exhibit (See Appendix D.2 for key)

except for the north. The north wall is a large rock cliff about fifteen to twenty feet tall. The access inside in the north corner. In the middle is a large maple tree, '1', roughly thirty to fifty feet tall. A second tree, '2', about fifteen to twenty-five feet tall is to the north of the large maple. A large branch, '3', is at a forty-five degree angle between the base of '2' and about ten feet up on '1'. To the south are two hammocks, twenty feet and fifteen up. The latter hammock is separated by a moat and was seldom used. The keeper access, '@,' is in the northeast corner. The exhibit is roughly sixty feet long (north/south) and between six and twelve feet wide (east west). Figure 10c is a photo of the indoor and outdoor exhibit.

Figure 10c.1: Indoor Exhibit at WPZ, with I (above) and II (below).

Figure 10c.2: Outdoor Exhibit at WPZ, with one the trees (above) and the moat (below).

There are two individuals at WPZ, Simon and Sutera. Simon was born July 18, 1980 at Cincinnati and received by WPZ June 3, 1982. Simon's long-time mate, Sai Buri, died December 18, 1997 of gastrointestinal cancer. Sutera, born February 7, 1992 at the Gulf Breeze Zoo, Florida, was brought to WPZ on February 12, 1998. The two had been introduced in the same exhibit within a month of my observations (Shewman 1998, personal communication). Figure 10d is a photo of Simon and Sutera.

Figure 10d: Sutera (Left) and Simon (right) at WPZ (WPZ Website 2004).

VI. Analysis

Daily maintenance activities, based upon IRFs, were divided into five categories: eating, locomotion, play, resting, and vocalizing. Figure 11 is adapted from Chivers (1974:141)

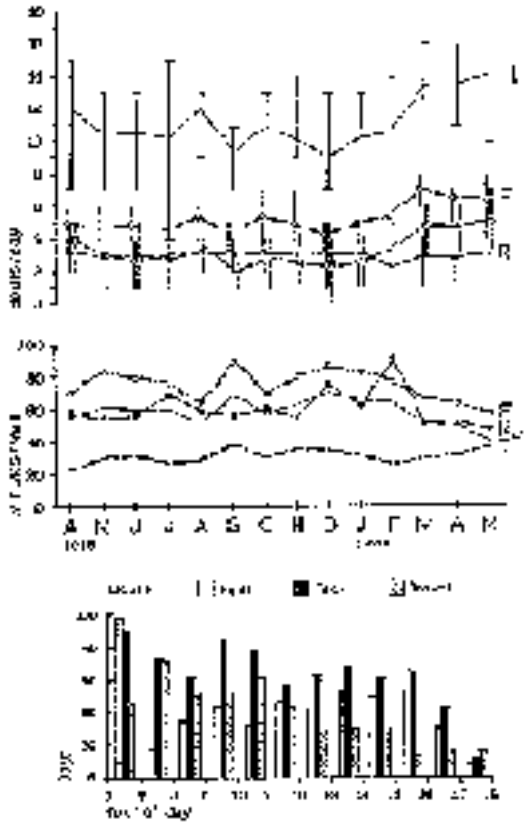

Figure 11: (a) The mean number of activity bouts/day — overall, rest feed, and travel; (b) the mean duration of bouts in each month at Kuala Lompat, and (c) the frequency of incidence of bouts of each maintenance activity in each hour of the day during the study (adapted from Chivers 1974:141).

in order to compare feral results to captivity. Figure 12 displays daily maintenance activities among captive Siamang. According to Chivers (1974) "average daily activity time was divided into 11.7 bouts, of which 3.5 (30%) were rest, 5.1 (44%) were feed, and 3.1 (26%) were travel" (Chivers 1974:140). In captivity, the time spent resting includes

Individual Daily Maintainence Activities (Rest, Eat, Locomotion, Voclaizaiton, and Play) — at SDZ, WPZ, SFZ, and CMZ (%)

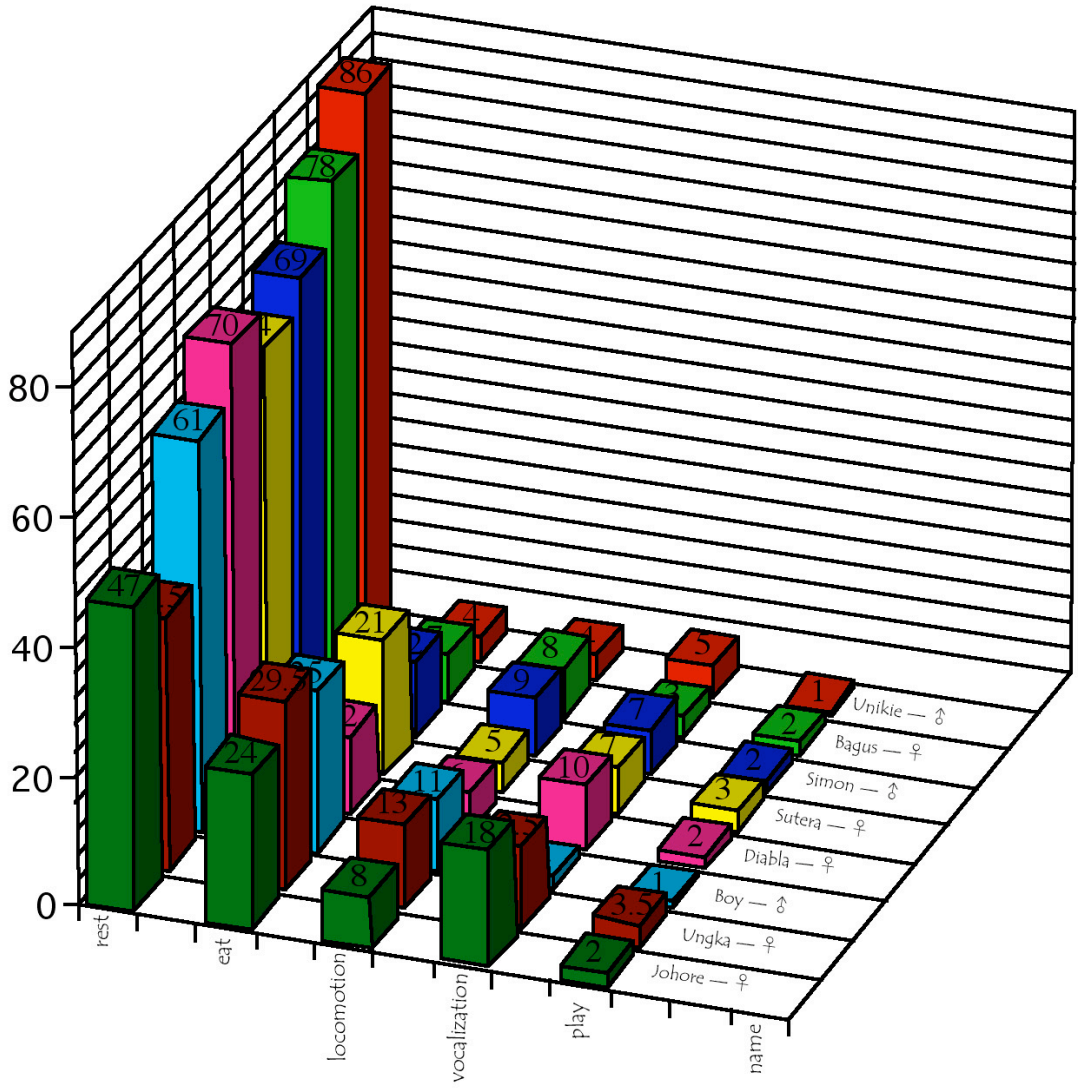

Figure 12: Daily Maintenance Activities at SDZ, WPZ, SFZ, and CMZ

the majority of time spent traveling. Therefore, locomotion accounts for little of daily maintenance activities because the need to travel is diminished.

Chivers (1974) observed morning vocalizations on 65% of the days. I observed morning vocalizations at SDZ 66% of the days; 75% of the days at SFZ; and 90% of the days at WPZ. At CMZ morning vocalizations occurred 44% of the days. Orgeldinger

(1997) cites a mean of 4.7% of time spent vocalizing in captivity, while Figure 12 shows a mean of 7.4%. Overall, the results are consistent with feral findings.

The discrepancy between Chivers, CMZ, and other captive exhibits results from the group composition, and the exhibit environment. Because the group consists of two females at CMZ it less likely to call than if a male were present, or a newly formed pair at WPZ (Aldrich and Chivers 1973; Palombit 1994a). Moreover, the CMZ exhibit is dark and simplistic. M. Goustard (1972:139) comments "light is one of the stimuli which causes them to call. Animals enclosed in a darkened cage do not call. They emit only a few segments from deep inside the cage." While addressing the influences of physical conditions Goustard makes the following observations:

> We have not found any relationship on the one hand between the number of elements, the total duration of a display, the total duration of inter-segments of a call, and, on the other hand, the temperature and barometric pressure. It could be that light and hygrometry [atmospheric conditions] have an effect. Generally, it does not appear that the presence of the physical conditions have a great influence on the temporal factors" (Goustard 1972:147).

The weather has an indirect affect upon vocalization onset. At CMZ vocalizations did not occur on the three days it snowed. At WPZ, however, vocalization did occur when it rained. This, too, is consistent with feral observations ; the weather had limited daily affects upon vocalizations (see Table 4, page 14). Chivers (1974) reports that vocalizations among Siamang groups occurred, on average, twenty minutes later on cloudy days. The Siamang at CMZ and SFZ showed a similar pattern, with vocalizations occurring, on average, thirty minutes later on cloudy days, while little variation occurred at SDZ and WPZ due to the weather. Table 5 displays information regarding the number of screams per minute and the average duration on captivity (see also Table 3, page 13).

Table 5: Siamang call characteristics in Captivity.

Zoo	Call dura-tion, min. (avg.)	Male, average number of screams per 1 minute (1:1) %	Male, average number of screams per 2 minute (1:2) %	Male, average number of screams per 3 minute (1:3) %	Female, average number of bark series (whut) and bark (vocl)
CMZ[1]	13.6				11—7
SDZ (Unkie)	22.0		71	29	13—6
SFZ (Boy)	18.8	19	59	22	21—8
WPZ (Simon)	15.9	52	46	2	20—7
Total	17.6	35	58	18	16—7

[1] Two females at CMZ (no screams recorded).

The seasonal variation of vocal bouts in feral locales reflects an increase in food availability at the start of the rainy season. For that reason more calling bouts were recorded in the dry season. Increased food availability is not a factor in captivity, since the animals are given the same quantity of food daily. Chivers (1974:267) makes the following comments about seasonal variation among gibbon and Siamang vocalizations:

> The concerted group calls, common to both Siamang and gibbons, are important in communication between social groups. Siamang groups called later in the day, less often, and sequentially, with greater seasonal variations. Siamang calls started between 0700 and 0900 h on 71% of days, whereas gibbon calls started between 0600 and 0800 h on 69% of days — about 1 h earlier on average.

Calling bouts at the four captive sites typically occurred just after 0900h and before 1130h. Perhaps the difference is evident in the daily activities. In feral contexts feeding begins just after sunrise, whereas in a captive context feeding does not occur before 0900h, resulting in the morning bout occurring later than in feral contexts. The delayed onset time reflects the time that the individuals are introduced into their exhibits. At SDZ and WPZ the zoo opens at 0900h and 0930h, respectively, and the animals are placed into their exhibits by 0800h. At CMZ and SFZ the animals spend the majority of their time in the exhibit. Even though sunrise may be as early as 0600h on some days, the sunrise appears belated, and therefore daily activities start later because feeding cannot occur until the food is provided. When the Siamang are first introduced to the exhibit each day a vocal bout is not uncommon, but I was unable to observe such bouts (Bates 1998, personal communication; Shewman 1998, personal communication).

The exhibit environment had a direct effect upon vocalization causation. At WPZ vocalizations occurred nearly one hundred percent of the mornings because every time they went outside vocalizations occurred, sometimes more than once. This may also be the result of a newly formed pair bond between Simon and Sutera. Furthermore, Simon spent larger amounts of time at the window vigilantly observing human visitors and his vocalizations were easily induced by the keepers. At SDZ vocalizations often occurred as an alarm to circling hawks over the zoo, and at SFZ as a dual between the two groups on the east and west ends in which the loudest group wins. The bouts at SFZ often occurred between vocal bouts by exhibit East, and were perhaps diminished by the presence of Storm (see page 15 and Orgeldinger 1997). At CMZ vocalization occurred as a response to the gibbons; “close proximity of gibbons enclosures leads to a higher frequency and high amount of territorial defense that can be stressful” (Orgeldinger 1997:323)

Intra-group distance in captivity is similar to feral observations (cf. Table 2, page 10). Table 6 displays mean distance between individuals, based upon results from IRFs, as both a percentage and a number The decreased time spent touching each other between Boy and Diabla at SFZ, and Simon and Sutera at WPZ implicate a couple of possibilities. At SFZ, Boy and Diabla are brother and sister who happened to have an infant because Boy's sexual productivity was not noticed in time (Pfirrmann 1998, personal communication). At WPZ, during my observation period Simon and Sutera had recently been introduced and were still getting to know each other (Shewman 1998, personal communication). In both cases, like in feral locales, the average distance between any two individuals is hardly greater than ten meters (Chivers 1976; Palombit 1994b).

Table 6: Mean Intra-distance in captivity.

	Individuals at Respective Zoos							
	Cheyenne Mt[1]		San Diego[2]		San Francisco[2]		Woodland Park[3]	
	Johore	Ungka	Unkie	Eloise	Boy	Diabla	Simon	Sutera
IRF Intra-distance value (#)								
1 (touching)	40	39	83	119	30	34	12	7
2 (within reach)	22	31	126	135	114	88	75	47
3 (same cage)	143	155	147	112	206	223	197	203
IRF Intra-distance value (%)								
1 (touching)	19	17	23	33	9	10	4	3
2 (within reach)	11	14	35	37	32	25	26	18
3 (same cage)	70	69	42	30	59	65	70	79
Total, min.	205	225	356	363	350	345	284	257

[1] 17 IRFs; [2] 25 IRFs; [3]22 IRFs (all per individual)

VII. Conclusion and Discussion

The exhibit environment proves fundamental to Siamang vocalization onset in captivity. Two factors contribute varying degrees of causation: the immediate environmental stimulation and an indirect affect of the weather. The stimulational exhibit functions as a territory whereas the traditional lacks the impetus to actively defend. WPZ provides the most naturesque exhibit, while CMZ lacks any environmental stimulation; both SFZ and SDZ comprise the middle ground of the spectrum.

The immediate stimulation seemed to be the same for both captive and feral contexts. Vocalizations occurred 60% (or greater) of the days, and calling bouts occurred, typically, between 0900h and 1200h. At CMZ 66% of the time a calling bout followed the onset of gibbon vocalization. Chivers (1974:267) cites a similar percentage:

> Group calls (bouts) in both species lasted about 15 min., but in Ulu Sampan gibbon calls were longer, where a higher proportion were male only. 64% of gibbon calls occurred before 0900 h, and 60% of Siamang calls were between 0900 and 1200 h in Ulu Gombak in 1968. Gibbon groups called twice in one day more often than Siamang.

CMZ was the only zoo with gibbons, who vocalized many days at or around 0900h and again at or around 1100h, while the Siamang vocalized only once or not at all. More often than not, the Siamang responded to the gibbon.

The weather, as mentioned above, had an indirect affect on Siamang vocalization, and, in fact, was consistent with feral observations (Chivers 1972, 1974). The time of onset on cloudy days was usually later than on sunny days. Certain days, however, at SFZ and WPZ the rain did not effect the onset time. The outside temperature had no affect at CMZ and WPZ because both indoor exhibits maintained a controlled temperature. The most significant difference between vocalization bouts on rainy and sunny days was the bout duration; typically bouts on rainy and cloudy days are twice as long because the rain muffles some of the sounds (Chivers 1974, 1976).

The onset of captive Siamang vocalizations are caused by similar feral stimulations: group cohesion, territory, and intra-group confrontations. Group cohesion is important for consistent calling bouts. Gibbon and Siamang monogamous pairs sing

together, often allowing one to solo and chime in after. If a monogamous pair were present at CMZ, it is more likely that more calling bouts would have been observed. The other exhibits include a pair-bond displayed varying degrees of cohesiveness. The newly-formed pair-bond at WPZ vocalized more frequently with increasing continuity; the pair at SFZ displayed continuity but lacked perfect cohesion; and the pair at SDZ vocalized with perfect continuity. Perfect continuity is defined as spontaneous commencement of a bout such that following a few faint resonations by the male the entire group begins to bark in unison (Chivers 1974; Tembrock 1972; Tyler 1990).

Territory reflects two inherent aspects spatio-temporal distribution: to actively advertise and to defend the territory (Chivers 1972, 1974; Tembrock 1972; Goustard 1972). Bouts performed by subadult and solitary males or females advertise a new territory, different from their natal territory, and serves to consort mates. Group calling bouts announce the presence of each family unit within their territory, and establishes intra-group cohesion among the family unit (Blake and Chivers 1973); Chivers 192, 1974; Goustard 1972; Tembrock 1972).

Intra-group confrontations are rare, but result from ecological stimuli. For example, Chivers (1974) reported that Siamang vocalizations were more intense around territories surrounded by logging activities. At SDZ vocal bouts as an alarm call when hawks circled were frequent. These bouts are usually longer than other calling bouts, and more often than not lack the general cohesion of inter-group bouts, but sometimes show an even greater continuity in timing between individuals.

The onset of Siamang vocalizations in captivity are the result of territorial advertisement, reinforced group cohesion, and inter-species defense. The Siamang may respond directly to conspecifics (gibbons, other Siamang, or other animals), and therefore advertise their own territory. A calling bout strengthens bonds between the individuals, and makes continuity more fluid between them. Territorial defense calling bouts were exhibited in response to allopatric species, but more commonly the result of ecological factors. Territorial defense also occurs because off in the distance they hear a familiar vocalization, but a positive visual identification cannot always be made, as at SFZ where the East and West exhibit were separated such that each group could hear the other but necessarily see the other.

Overall, the characteristics of the Siamang in captivity are consistent and similar to those observed in a feral context. The Siamang has adapted to the smaller territory and daily environmental stimulation. Daily maintenance activities tend to reflect a less active habitat; more time was spent resting and performing idle activities in captivity than in

feral locations, whereas more time was spent traveling to feeding stations in the wild than in captivity. Vocalization bouts in captivity were consistent with feral observations. The time of onset showed similar patterns relative to weather, typically beginning between twenty and thirty minutes later on cloudy days. The duration of the bouts also showed similar patterns for inter-group confrontations and group territory advertisement. The group exhibited greater continuity between members during responses to ecological factors.

The role of the exhibit environment coupled with group cohesion and active territorial defense reflects the degree of ecological stimulus. The WPZ exhibit provides a territory (in the outside exhibit) that can be defended by vigorous tree shaking. On the other hand, the CMZ exhibit lacks ecological stimulus to create an active territory. In between these two extremes, the SFZ and SDZ exhibits create a territory to defend but lack similar ecological stimulus as WPZ to establish an active territory.

In the coming century, if the role of zoological gardens continues to be conservation, education, and species survival plan research, then, to ensure the well-being of the animals and the success of captive breeding programs, an actively defended territory is fundamental. The zoological garden that establishes an exhibit that emulates the feral environment to the best of their ability provides an actual territory. This exhibit will not only behoove the animal well-being, but also educate the public about the complete ecosystem in which the animal occupies in the wild, and increase awareness of world conservation efforts.

VIII. Appendix(es)

Appendix I: Exhibit Drawing Keys

A. Cheyenne Mountain Zoo

1 = log upright left cage
2 = log at 45˚ angle from **4**
3 = log at 15˚ angle from **BS**
4 = center log, upright between ceiling and floor
5 = log across top, between **1** and **4**, and over **3**
A = food basket left, closer to **1**
B = food basket right
BD = service area access for zoo personnel
BS = back shelf
F = foreground
G = ground
T = drinking faucet
***** = ceiling skylight grate
= access to holding area

B. San Francisco Zoo

A-C = south side
D-F = north side
G = rope from SE corner through A, D, E, and F to #
H = rope from SE corner through A, B, and C to SW corner
T = drinking fountain
1 = branch in corner
2 = hammock
3 = branch in F
4 = branch in E
5 = rope off 4 to top in E
w-z = various ropes of middle bar
= shelf
***** = keeper access door
® = Siamang access to inside holding
& = food bins

C. San Diego Zoo

A = vertical log (W)
B = vertical log (E)
1-8 = other logs at various angles on A
15,16 = logs horizontal to 5 and 6
9-14 = other logs at various angles on B
u-w = ropes off B
x-z = ropes off A
C-F = quadrants for ground
a-g = metal bars (not shown) occur at angles 1-16

D. Woodland Park Zoo

1 (Indoor)

I-II = north and south sections of exhibit
a-d = windows
¡! = nook in branches
® = higher nook in branches
***** = hammock
@ = access to bedroom
% = access to outside
& = keeper access
T = drinking fountain

2 (Outdoor)

1 = center maple tree
2 = other maple tree
3 = branch at 45˚ angle between 1 and 2
***** = hammock
@ = cliff and keeper access
% = access inside

Appendix II: IRF Context and Behavioral Codes

This appendix is an explanation of the four letter context and behavior codes used in IRFs. There are six context codes. The behavior codes are divided into five categories: eat, locomotion, rest, play, and vocalize.

Contexts:

AFFI: Affinitive Behavior: This context includes friendly and affinitive behavior directed toward another animal by the focal animal e.g. embracing, grooming, kissing, sharing food, or sitting quietly among a group.

AGGR: Agnostic Behavior: This context is scored when the focal animal is directing any threatening, aggressive, or intensely dominating behavior toward another Siamang.

BAOB/MSOB: Bad Observation/Missed Observation: Both these contexts are scored when the observer is unable to see the animal clearly (BAOB) or is distracted long to be unable to make an observation (MSOB). Strictly speaking these are not contexts, but errors and/or things beyond the control of the observer.

PUOR: Public Orientation Behavior: This context is scored when the focal siamang's attention or visual orientation is clearly oriented toward the viewing public, zoo keepers, or other employees. This is most common when a Siamang is looking for a keeper while waiting for food, etc.

SIOR: Siamang Orientation Behavior: This context is the same as PUOR but attention or visual orientation is clearly oriented at another Siamang. It is common during grooming sessions and aggressive displays and mild displacements.

SONS: Solitary-Nonsocial Behavior: This context is scored when an individual distances himself others and does not interact. It is usually scored during feeding, locomotion, resting (except grooming), and vocalization.

Behaviors:

EAT: (3 codes)

FODM/H: This is technically two codes, but since both were simultaneous were scored as both. This was scored when food was held in the hand or mouth, and was chewed. Allowable contexts: SONS, SIOR, PUOR.

FORG: This was scored when the focal animal was searching or foraging for food in the basket. Allowable contexts: SONS.

DRKH/M: This was scored when the focal animal drank water droplets from the back of the hand. Allowable contexts: SONS.

LOCOMOTION: (3 codes)

SWNG: This was scored when the focal animal was swinging on ropes. Allowable contexts: SONS.

BRAC: This was scored when the focal animal was brachiating on either ropes or branches. Allowable contexts: SONS.

BPWR: This was scored when the focal animal ran or walked across the ground bipedally with the arms above the head. Allowable contexts: SONS.

REST: (11 codes)

HANG: This was recorded when the focal animal was hanging from either a branch or a rope. Allowable contexts: SONS, SIOR, PUOR, AFFI.

PEEP: This was scored when the focal animal was observed peeing. Allowable contexts: SONS.

SITT: This was scored when the focal animal was observed sitting on either a branch or a rope. Allowable contexts: SONS, SIOR, PUOR.

BPST: This was scored when the focal animal was standing any in the enclosure bipedally. Allowable contexts: SONS, SIOR, PUOR, AFFI.

WTCH: This was scored when the focal animal was observed watching objects and people or each other. Allowable contexts: SONS, SIOR, PUOR.

GRSF: This was scored when the focal animal was observed grooming herself. Allowable contexts: SONS, SIOR, PUOR.

GRMT: This was scored when the focal animal was observed being groomed by another. Allowable contexts: AFFI, PUOR.

GROT: This was scored when the focal animal was observed grooming another individual. Allowable contexts: AFFI.

IDAW: This was scored when the focal animal was observed lying or idling in a recumbent position anywhere in the enclosure. Allowable contexts: SONS, SIOR, PUOR.

SKTH: This was scored when the Ungka sucked her thumb. Allowable contexts: SONS, SIOR, PUOR.

STND: This was scored when the focal animal was observed standing and hanging on to something. Similar to BPST but dependent upon an inanimate object (branch, cage, rope, etc.). Allowable contexts: SONS, SIOR, PUOR, AFFI, AGGR.

PLAY: (8 codes)

THRT: This was scored when the focal animal was observed making an open-mouth threat. Allowable contexts: AGGR.

WRST: This was scored when the focal animal was observed wrestling with another individual. Allowable contexts: AFFI, AGGR.

CHCK: This was scored when the focal animal and another was observed playing the displacement game of "chicken." Allowable contexts: AFFI, AGGR, SIOR.

BITE: This was scored when the focal animal was observed biting another individual. Allowable contexts: AGGR.

PULL: This was scored when the focal animal was observed pulling an extremity or body of another individual. Allowable contexts: AFFI, AGGR.

SLHT: This was scored when the focal animal was observed slapping and/or hitting another individual. Allowable contexts: AGGR.

CHAS: This was scored when the focal animal was observed chasing another around the enclosure. Allowable contexts: AFFI, AGGR.

HOLD: This was scored when the focal animal was observed holding onto to an object or another individual. Allowable contexts: AFFI, AGGR, SONS, SIOR, PUOR.

VOCALIZATION: (7 codes)

VOCL: This was scored when the focal animal was observed barking. Allowable contexts: SONS, SIOR, PUOR.

RESN: This was scored when the focal animal was observed resonating or filling the laryngeal sac. Allowable contexts: SONS, SIOR, PUOR.

GRNT: This was scored when the focal animal made grunts (unthaw!). Allowable contexts: AFFI, SONS, SIOR, PUOR.

CHRP: This was scored when the focal animal was observed chirping. Allowable contexts: SONS, SIOR, PUOR.

WHPR: This was scored when the focal animal was observed whimpering. Allowable contexts: AFFI, SONS, SIOR, PUOR.

SCRM: This was scored when the focal animal was observed in a vocal bout and applies to males only. Allowable contexts: SONS, SIOR, PUOR.

WHUT: This was scored when the focal animal was observed in vocal bout and applies to females only. Allowable contexts: SONS, SIOR, PUOR.

IX. Bibliography

Aldrich, Blake and David Chivers
(1973). "On the Genesis of a Siamang Group." *Am. J. Phys. Anthro.* 38:631-636.

Altman, J.
(1974). "Observational study of behaviour: sampling methods". *Behaviour.* 49:227.

Bramblett, C. A.
(1994). *Patterns of Primate of Behavior: Second Edition* . Prospect Heights, IL: Waveland Press, Inc.

Bates, M.
(1998). San Diego Zoological Garden Primate Keeper. Interview with Author October 9, 1998.

Blum, D.
(1994). *The Monkey Wars.* NY: Oxford Univ. Press.

Brewer, M.
(1997). *The Onset of Vocalization Among Hylobates (Symphalangus) syndactylus at Cheyenne Mountain Zoo.* Paper for AN306 Primatology, The Colorado College presented March 3, 1997.

Carpenter, C.R.
(1938). "A Survey of Wildlife Conditions in Atjeh, North Sumatra." *Netherlands Commission of International Nature Protection* , vol.12:1-33.

(1940). "A Field Study in Siam of the Behavior and Social Relations of the gibbon, *Hylobates lar* ." *Comp. Psychol. Mongr.* 16:1-212.

———
(1998). Cheyenne Mountain Zoo. http://www.cmzoo.org. visited 15 Feb. 1999.

Chivers, D.J.
(1972). "The Siamang and the Gibbon in the Malay Peninsula." In *Gibbon and Siamang: A Series of Volumes on the Lesser Apes* . (Duanne M. Rumbaugh, ed.). NY: S. Karger. vol.1:103-136.

(1974). *The Siamang in Malaya: A Field Study of a Primate in Tropical Rain Forest* . NY: S. Karger.

(1976). "Communication within and between Family Groups of Siamang (*Hylobates syndactylus*)." *Behaviour*. 57:116-133.

Cohen, J.M and M.J. Cohen
(1960). Penguin Dictionary of Quotations. NY: Penguin Books, Ltd.

Colahan, J.
(1997). Personal Interview with Author January 30, 1997. Primate Keeper at Cheyenne Mountain Zoo.

Conway, W.
(1995). "Zoo Conservation and Ethical Paradoxes." *In* Ethics of the Ark: Zoos, Animal Welfare, and Wildlife Conservation. (Bryan G Norton et. al. ed.) Washington DC: Smithsonian Inst. Press. pp.1-9.

Cowishaw, G.
(1992). "Song Function in Gibbons." *Behaviour* 121(1-2):131-153.

Crowley, W.
(1995). *The Woodland Park Zoo Guide*. Seattle: Crowley Associates, Inc.

De Vaal, F.
(1989). *Peace Making Among Primates*. Cambridge, MA: Harvard Univ. Press.

Ellefeson, J.O.
(1967). "Territorial Behavior in the Common white-handed gibbon, *Hylobates lar*." In *Primates: Studies in Adaptation and Variability* . (P.C. Jay, ed.). NY: Holt, Rinehart and Winston. pp.180-199.

Fox, G.
(1972). "Behavior of a Siamang Group in Milwaukee Zoo." *Folia Primat*. 18:122-139.

Geissman, T.
(1986). "Mate Change Enhances Duetting Activity in the Siamang Gibbon (*Hylobates snydactylus*)." *Behaviour* 96(1-2):17-27.

Geissman, T. and A. M. Hulftegger
(1994). "Olfactory communication in gibbons?" *In* Current Primatology, Vol. II: Social Development, Learning, and Behaviour. (J.J. Roeder; B. Thierry; et. al. eds.). Strasbourh: Univ. Louis Pastuer. pp.199-206.

Gittins, S.P. and J.J. Raemakers
(1980). "Siamang, Lar, and Agile Gibbons." In *Malayan Forest Primates* . (David J. Chivers, ed.). NY: Plenum Press. p.63-106.

Goodall, J.
(1971). *In the Shadow of Man*. London: Collins.

Goustard, M.
(1976). "The Vocalizations of Hylobates." In *Gibbon and Siamang: A Series of Volumes on the Lesser Apes* . (Duanne M. Rumbaugh, ed.). NY: S. Karger. vol.4:136-166.

Groves, C.P.
(1972). "Systematics and Phylogeny of Gibbons" In *Gibbon and Siamang: A Series of Volumes on the Lesser Apes* . NY: S. Karger.(ed. D.M. Rumbaugh). vol.1: pp. 2-89

Hancocks, D.
(1995). "Lions and Tigers and Bears, Oh no!". *In* Ethics of the Ark: Zoos, Animal Welfare, and Wildlife Conservation. (Bryan G Norton et. al. ed.). Washington DC: Smithsonian Inst. Press.pp.31-7.

Hill, G.
(1967). "Gestation Period for the Siamang." *Int. Zoo Yb*. 7:93-94.

Jay, P.C.
(1968). *Primates: Studies in Adaptation and Variability* . NY: Holt, Rinehart and Winston.

Jolly, A.
(1985). *Ecological Primate Behavior*. NY: Macmillian.

Kloss, C.B.
(1929). "Some Remarks on the Gibbons, with the Description of a New Sub-species." *Proc. zool. Soc. Lond.* 1929:113-127.

Marler, P.
(1968). "Aggregation and Dispersal: Two Functions in Primate Communication." In *Primates: Studies in Adaptation and Variability* . (P.C. Jay, ed.). NY: Holt, Rinehart and Winston. pp.420-438.

Mason, W.A.
(1968). "Use of Space by *Callicebus* groups." In *Primates: Studies in Adaptation and Variability* . (P.C. Jay, ed.). NY: Holt, Rinehart and Winston. pp.180-199.

Miller, E
(1992). "The Effect of Captivity Upon *Hylobates (Symphalangus) snydactylus* at Cheyenne Mountain Zoo." Paper for AN306 Primatology, The Colorado College presented December 19, 1992.

Morgan, E.
(1995). *The Descent of a Child.* NY: Oxford Univ. Press.

Napier, J.R. and P.H. Napier
(1967). *The Handbook of Living Primates* . NY: Academic Press.

Norton, B.G., et. al.
(1995). *Ethic on the Ark: Zoos, Animal Welfare, and Wildlife Conservation.* Washington DC: Smithsonian Inst. Press.

Orgeldinger, M.
(1991). "Siamang (Hylobates syndactylus) in captivity: An overview. *Int. Zoo News.* 38(6):5-15.

(1993). "Observations on Siamang (Hylobates syndactylus) behaviour in zoological gardens with special regard to social behaviour. *Primate Report.* 35:91.

(1996). "Territorial behaviour in captive Siamang (Hylobates snydactylus). *Primate Report.* 44:34-5.

Philippart, M.
(1991). "Captive Siamang Monogamous Pairs at the Cheyenne Mountain Zoo." Paper for AN306 Primatology, The Colorado College presented March 6, 1991.

Palombit, R.
(1994a). "Pair Bonds in Hylobatids: Implications Regarding Monogamous Social Systems." *Behaviour.* 128(1-2):65-101.

(1994b). "Pair Copulations in a Monogamous Ape." *Animal Behaviour.* 47:721-3.

Pfirrmann, H.
(1998). Primate Keeper, San Francisco Zoo. Interview with Author September 26, 1998.

Preuschoft, H., Chivers, D.J., Brockelman, W.Y., and Creel, N.
(1984). *The Lesser Apes: Evolutionary and Behavioral Biology* . Edinburgh: Edinburgh University Press.

Raffles, T.S.
(1821). "Descriptive catalogue of a zoological collection, made on account of the Honourable East India Company, in the Island of Sumatra and its vicinity". *Linn. Trans.* 13:239-274

Richard, A. F.
(1985). *Primates in Nature* . NY: W.H. Freeman and Company.

Rumbaugh, D.M.
(1972). *Gibbon and Siamang: A Series of Volumes on the Lesser Apes* . NY: S. Karger.

———
(1998). San Francisco Zoo. http://www.sfzoo.com. visited 15 Feb. 1999.

Schultz, A.H.
(1933). "Observations on the Growth Classification and Evolution Specialization of Gibbons and Siamang." *Human Biology* 5:212-255, 385-428.

Shepherdson, D.J., J.D. Mellen, and M. Hutchins
(1998). *Second Nature: Environmental Enrichment for Captive Animals.* Washington DC: Smithsonian Inst. Press

Shewman, H
(1998). Asian Forest Primate Keeper, Woodland Park Zoo, Seattle, Washington. Interview with Author June 13, 1998.

Soo-Hoo, C.
(1966). "A Brief Note on the Birth of a Siamang." *Int. Zoo Yb.* 1966:147.

Tembrock, G.
(1972). "Sound Production of *Hylobates* and *Symphalangus* ." In *Gibbon and Siamang: A Series of Volumes on the Lesser Apes* . (Duanne M. Rumbaugh, ed.). NY: S. Karger. vol.3:176-205.

Thomas, O.
(1908). "On Mammals from the Malay Peninsula and islands". *Ann. Mag. Nat. Hist.* 2(8):301-6.

Tyler, J.W.
(1990). "Comparison of the Species-typical Duet of Three Siamang (*Hylobates syndactylus*) Pairs. Psychology Independent Study: North East Louisiana Univ., Monroe, LA.

———
(1998). Woodland Park Zoo. http://www.zoo.org. visited 15 Feb. 1999.
(2004). http://zoo.org/gallery/mammals/primates/siamang/slide3.jpg. Visited December 7, 2004.

———
(1999). Zoological Society of San Diego. http://www.sandiegozoo.org. Visited 15 Feb. 1999.