



Longitudinal Patterns of Reproduction in Wild Female Siamang (*Hylobates syndactylus*) and White-Handed Gibbons (*Hylobates lar*)

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*I present the 6-year reproductive histories of three wild female siamang (*Hylobates syndactylus*) and four white-handed gibbons (*Hylobates lar*) at the Ketambe Research Station (Sumatra, Indonesia). Reproductive output varied considerably among females. Two females failed to gestate: both were nulliparous young adult *H. lar*, one of which remained unpaired for 4 years after dispersing from her group, while the other lost her recently acquired mate to another female. Only one—a white-handed gibbon—gave birth more than once, yielding interbirth intervals of 22 and 31 months. Pair bond stability or reduced interspecific feeding competition or both factors may have contributed to the brevity of these intervals. The other females—one *H. lar*, and three *H. syndactylus*—each gave birth once, suggesting minimum interbirth intervals exceeding 4–5 years (*H. lar*) and 3 years (*H. syndactylus*) in these individuals. Even given the pronounced variation observed among *H. lar*, these data suggest that interbirth intervals may often exceed the 2- to 3-year interval commonly attributed to these two species. Sources of reproductive failure were 1) maternal abandonment of the neonate due to impaired ability to provide maternal care (*H. syndactylus*), (2) premature or stillbirth (*H. syndactylus*), and (3) pregnancy termination (*H. lar*). These data and a review of information on longevity and age at menarche suggest that the actual lifetime reproductive output of a siamang or white-handed gibbon female may often fall far short of the 10 offspring/lifetime originally proposed for these species. Indeed, females may rear as few as five offspring to weaning in a lifetime, which is a figure reminiscent of the reproductive potential of some pongids. Finally, variance in*

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female reproductive success is higher than expected in these monogamous species, which suggests that females (and males) are under strong selective pressure to exert mate choice, possibly through acquisition of (new) mates and extrapair copulations. Future research must clarify the availability of opportunities for paired adults to engage in these sociosexual behaviors.

KEY WORDS: *Hylobates syndactylus*; *Hylobates lar*; reproduction; monogamy.

INTRODUCTION

Longitudinal data on variation in reproductive success are critically important to understanding the evolution of mating systems of long-lived, iteroparous organisms such as mammals. Such long-term field studies of individually recognizable mammals have only recently been undertaken and have focused primarily on polygynous systems (Clutton-Brock, 1988a). Very little is known about reproduction of wild monogamous mammals. As Hrdy (1981) points out, data describing the long-term pattern of female reproduction are extremely useful to understanding how the selective effects of direct paternal care and the spatiotemporal abundance and distribution of females influence the evolution of mating systems in general (*sensu* Emlen and Oring, 1977; Davies, 1991) and monogamy in particular (Wittenberger and Tilson, 1980; Barlow, 1988). For example, monogamous female canids appear capable of reproducing at higher rates than similarly sized polygynous mammals, which may enhance the benefit/cost ratio of monogamy to males (Clutton-Brock, 1989). Increased scrutiny of reproduction in monogamous mammals is further recommended by recent demonstrations of unexpectedly high intraspecific variation in mating and social behaviors in monogamous birds (Mock, 1985).

The gibbons (Hylobatidae) are among the most studied monogamous mammals, but reproduction of wild individuals is poorly documented. In the relative absence of such data, it has been necessary to use the demographic structure of gibbon populations to infer individual reproductive patterns. For example, Carpenter (1940) concluded that interbirth intervals for female white-handed gibbons were approximately 2–3 years, since that appeared to be the typical age difference among immatures in gibbon groups. That figure subsequently yielded an estimated lifetime reproductive potential of 10 offspring for the average female.

Recent observations of movements of both adults and immatures between groups during mate replacement and pair formation in wild hylobatids challenge the assumption that all immatures of a family are the shared offspring of the resident adult heterosexual pair (Palombit, 1994a).

Thus, the collection of longitudinal reproductive data based on direct observation of individual females becomes crucial.

Although he suggested that reproductive parameters such as interbirth intervals might vary, Carpenter's (1940) preliminary analysis has not been improved upon substantively, in part because current knowledge of reproduction, longevity, and offspring survival in the wild is only slightly better than it was when he conducted his pioneering study in 1937. Current longitudinal reproductive data from the field are limited to a few groups of sympatric white-handed gibbons and siamang observed discontinuously for 10 years in peninsular Malaysia (Chivers and Raemaekers, 1980) and 10 groups of agile gibbons monitored for relatively short periods over 6 years in western Borneo (Mitani, 1990). Many basic features of reproduction in the Hylobatidae remain largely obscure.

I attempt to redress, in part, this deficiency for two species, the white-handed gibbon (*Hylobates lar*) and the siamang (*Hylobates syndactylus*). I present the reproductive histories of wild females for more than 6 years and review current reproductive data for these species in the wild and captivity. This information permits a preliminary analysis of reproductive potential, interbirth intervals, sources of reproductive failure, and variance in female reproductive success in these species.

METHODS

Study Area

The research was conducted at the Ketambe Research Station (3°40' N, 97°40' E) in the Gunung Leuser National Park, northern Sumatra, Indonesia. The approximately 300-ha study area lies between the confluence of the Alas and Ketambe rivers. The predominant forest is mixed-dipterocarp, primary lowland rain forest of the "hill" or "upland" type (Laumonier, 1990), which occupies a series of terraces rising from alluvial areas in the north (ca. 350 m a.s.l.) to the slopes of mountains (>600 m) to the south (van Schaik and Mirmanto, 1985). The territories of all hylobatid study groups are situated on the lower terraces (<600 m). Detailed descriptions of the study area are provided by Rijksen (1978), van Schaik (1986), and Palombit (1992).

Subject Females

I studied seven females from four groups. Four of the females are white-handed gibbons: AY and her putative daughter AA (from Group A)

and females GM and her putative daughter GP (from Group G). I monitored three siamang females: PN from Group P and CJ and her putative daughter CO (from Group C). All females were fully habituated to human observers and individually recognizable.

Parous Adult Females. Four females—siamang CJ and PN and white-handed gibbons AY and GM—were primi- or multiparous adults at the beginning of the study. All four females possessed pendulous nipples suggestive of past infant-rearing, and siamang PN and white-handed gibbon AY were in fact carrying and nursing dependent infants at that time. Additionally, each female was paired to an adult male with which she defended a territory and duetted. All but one of these females acquired a new mate some time during the study (Palombit, 1994a). Observed labial eversions in all four females provided additional evidence of reproductive cycling.

Nulliparous Young Adult Females. Three females—siamang CO and white-handed gibbons GP and AA—were classified initially as nulliparous subadults at the beginning of the study. At that time all three resided in groups with a single adult heterosexual pair, were slightly smaller in body size (assessed visually) than the paired, adult females, and possessed prominent but distinctly nonpendulous nipples.

The reproductive histories of these three females are included here because they became sexually mature adults during the course of the study. All of them attained body sizes similar to or greater than the parous females. They all emigrated from their putative natal groups during the second year of study. Dispersal coincided with pair formation for two of these females (Palombit, 1994a). One of them—siamang CO—gave birth 18 months after emigrating from her putative natal group, which suggests that she was sexually mature at least 5 months after this event, given a gestation period of 7.5–8 months (Hall, 1967; LaMalfa, 1969; Geissmann, 1991).

Regular cycles of labial eversions in the other two females provide additional evidence of sexual maturity and reproductive activity. Although Schultz (1938, 1973) previously discounted the existence of regular changes in the external genitalia of female gibbons, observations of live, captive females have documented cyclical variation in the color, eversion, and turgidity of the urethral eminence, labia minora, and vaginal wall in *Hylobates lar* (Berkson and Chiacumpa, 1969; Dahl and Nadler, 1989, 1992) and *Hylobates hoolock* (Matthews, 1946). Fewer data are available for *H. syndactylus*, but Chivers (1974, p. 220) described vulvular eversions and color changes “from black to white to red to white and then black again” in wild adult females. These swellings are much less pronounced than those of primates that possess the naked sexual skin surrounding the perineum

(Rowell, 1972; Dixon, 1983), but they are conspicuous enough to act potentially as visual signals of female reproductive state or receptivity. Although much of the underlying physiology and anatomy is poorly understood, genital changes in *H. lar* apparently track the 30-day menstrual cycle (Breznock *et al*, 1977; Kollias and Kawakami, 1984; Nadler and Dahl, 1992). Synchrony of ovulation with maximal eversion has not been verified, but the reported coincidence of greatest labial turgescence and heightened breeding receptivity in captive females (Breznock *et al*, 1977; Kollias and Kawakami, 1984; Nadler and Dahl, 1992) is suggestive since sexual behavior typically peaks around time of ovulation in many primate species (Hrdy and Whitten, 1987; Dunbar, 1988). Chivers (1978) also noted covariation of copulation rate and genital color in one siamang female. Onset of swelling cycles appears to accompany menarche in *H. lar* (Carpenter, 1941; Berkson and Chaicumpa, 1969) and *H. hoolock* (Matthews, 1946). Although no developmental datum is available for *H. syndactylus*, it seems reasonable to assume tentatively that the initiation of cyclic vaginal eversions observed in adults is associated with the arrival or approach of sexual maturity.

Labial eversions occurred in the two originally nulliparous subadult white-handed gibbon females of this study—GP and AA. After 16 months of regular observation, GP exhibited eversion for the first time several weeks before her emigration from her group. AA showed no obvious change in external genitalia in the 16 months preceding her dispersal, but she clearly exhibited labial eversion on several occasions in subsequent postemigration years.

Evidence for Gestation

The birth of an infant is of course the most unambiguous (post hoc) sign of pregnancy, but typically there are other, conspicuous indications of pregnancy in nonhuman primates. Enlargement of the abdomen and mammae preceding birth occurs in gestating hylobatids under wild, seminatural, and captive conditions (Robinson, 1925; Sasaki, 1963; Badham, 1967; Berkson and Chaicumpa, 1969; Brody and Brody, 1974; Chivers and Chivers, 1975; Breznock *et al*, 1977; Kollias and Kawakami, 1984). In *H. lar* distension of the abdomen first becomes noticeable around 150–160 days after fertilization and is extremely prominent just before parturition—around 190–220 days (Kollias and Kawakami, 1984). I noted conspicuous abdominal distension 1–2 months before parturition in all five females that gave birth at Ketambe; prenatal mammary enlargement was also noticeable in one siamang and one white-handed gibbon. These pronounced physical

changes accompanying gestation were useful in recognizing one possible case of pregnancy termination among the subject females at Ketambe.

Infants. I measured two siamang infants shortly after birth. I weighed them via a Pesola 300-g hang scale with 10-g increments and used a standard metric tape for linear measurements.

Observation Period

I monitored the long-term histories of reproduction of subject females for > 6 years, from August 1985 through December 1991. My wife, two to five assistants, and I monitored females continuously through August 1988, during regular systematic follows (5–10 days/group/month). From September 1988 to December 1991, B. Putra Gayo conducted monthly group censuses. He continued to contact the study groups for a subsequent study of sympatric primates conducted continuously at Ketambe from November 1988 to March 1992 (Sterck, in preparation). I also censused all study groups for two 1-month periods in August 1988 and August 1990.

RESULTS

Pregnancies and Their Outcomes

Table I summarizes the reproductive histories of the seven subject females over 6 years. Only two of them failed to give birth or display the conspicuous signs of advanced pregnancy. Both of them were newly dispersed, nulliparous adult white-handed gibbons, one of whom (AA) remained an unmated, solitary floater occupying marginal habitat contiguous to her former group, while the other (GP) was deserted by her recently acquired pairmate (Palombit, 1994a).

Although the other five females gestated during the study, their reproduction was not equivalently successful. Only five of eight (63%) of the pregnancies among five females resulted in the live birth of a neonate that survived beyond the first month of life. Reproductive failure occurred in three ways: (1) maternal abandonment of the neonate; (2) apparent still-birth; and (3) pregnancy termination.

Maternal Abandonment: The siamang PN gave birth to a male infant in late November, 1987. Simultaneously, she contracted a debilitating disease that caused extreme lethargy and eventually death (Palombit, 1992). The infant, however, appeared normal and was active vocally and physically, climbing on and off her as well as suckling. The female abandoned him when he was approximately 10 days old by moving immediately away

Table I. Reproduction of Adult Female Hylobatids at Ketambe (August 1985–December 1991)

Female	Parity	Pair-bond status	No. of pregnancies	Pregnancy outcome
<i>H. syndactylus</i>				
PN	Parous adult	Paired; switched mate	1	Live birth, but neonate abandoned
CJ	Parous adult	Paired	1	1 premature birth: neonate dead
CO	Nulliparous young adult	Recently dispersed and newly paired	1	1 live birth
<i>H. lar</i>				
AY	Parous adult	Paired to same male	3	3 live births
GM	Parous adult	Paired; switched mate	1–2	1 termination; 1 live birth
GP	Nulliparous young adult	Recently dispersed, paired briefly to male	0	
AA	Nulliparous young Adult	Recently dispersed, unpaired floater	0	

from him when he climbed momentarily from her onto an adjacent liana during an autoplaysession. The infant screamed for the next 90 min, after which the rate of calling declined. Although the mother often oriented toward the infant when he screamed, and although the adult male of the group approached to ≤ 5 m of him, neither adult attempted to retrieve him. After 4 hr, the group traveled away, leaving him behind. No member of this group returned to the area where he had been left until over a week later.

Apparent Stillbirth: In August 1987 the female CJ gave birth to a male infant that showed no sign of life: clinging, movements of limbs, or vocalizations. The female occasionally licked the infant, but held him awkwardly by the neck, which suggests that he was dead or exceptionally weak. The mother brachiated very little on the morning of parturition, but when she did, she managed to carry the infant crosswise in her lap by cradling him in her tightly flexed thighs, as captive gibbons do with newborn infants that do not cling (Coolidge, 1933).

The infant fell from CJ to the ground around noon on the day of his birth, whereupon the mother descended to a canopy height of 12 m and looked downward. About 7 min later CJ traveled away from the area, leaving him dead on the ground.

Compared to the infant born to siamang PN, the developmental state of this infant's body suggests that he may have been born prematurely (Table II). For example, CJ's infant weighed only 240g within 24 hr of its birth, compared to 560g reported for a captive infant (Rumbaugh, 1967) and 500g for PN's infant, which was 5–13 days old at the time of measurement. Age differences between the infants of CJ and PN may be responsible for some physical differences at the time of measurement (Table II).

Pregnancy Termination: In late July, 1987 the white-handed gibbon female GM displayed the conspicuous physical characteristics of advanced gestation that always preceded parturition in the five females that gave birth. A high rate of copulation with her pairmate in the previous March and early April further support the deduction that she was pregnant. At the beginning of September, 1987, however, her previously distended abdomen and slightly swollen mammae were suddenly much reduced to the size they had been throughout 1986 and early 1987. As in other nonhuman primates (Mori and Dunbar, 1985; Turner *et al.*, 1987), this pronounced and sudden reduction in abdominal size may indirectly indicate pregnancy termination. GM did not show vaginal bleeding, like that which accompanies abortion in some Old World monkeys (Mori and Dunbar, 1985; Agoramorthy *et al.*, 1988), but Breznock *et al.* (1977) note that captive white-handed gibbon females may abort without any such physiological indications.

Table II. Physical Attributes of Two Male Siamang Infants

	Female CJ's infant ^a	Female PN's infant ^b
Body mass (g)	240	500
Body length (cm)	28	36
Breast circumference (cm)	12	17
Elbow to wrist (cm)	6	9
Body hair	Torso entirely naked; supraorbital hairs present, short hairs on scrotum	Head and dorsal surface of torso covered with long black hair; abdomen sparsely haired
Cranium	Occipital and parietal regions firm; crown has soft, concave depression	Entire cranium firm; no soft spot
Eyes	Left eyelid opens under slight pressure; right eyelid fused shut and will not open	Both eyes open

^aMeasurements taken on the day of birth (or stillbirth).

^bMeasurements taken on day infant abandoned by mother when infant was 5–13 days old.

Interbirth Intervals

Only one female, white-handed gibbon AY, gave birth more than once during 6 years to provide direct data on interbirth intervals. She gave birth in mid-July 1987, mid-May 1989, and mid-November 1991. Accordingly the two respective interbirth intervals are approximately 22 and 31 months.

The other four females gave birth only once during the 6 years of observation. Thus, while it is not possible to designate a precise interbirth interval, the timing of these births during the study allows an estimate of the minimum interbirth interval for each female:

- 1) The siamang CO's primiparous birth in June–July 1988 was not followed by an additional birth in the subsequent 41 months, which represents a minimum interbirth interval of 41 months.
- 2) The parous siamang CJ failed to give birth to a live infant during 35 months of observation though she had one stillbirth. Accordingly, her minimum interbirth interval exceeds about 3 years.
- 3) The siamang PN did not give birth to a live infant until the 27th month of observation. Given that PN was probably the mother of the older infant she was continually carrying at the beginning of the study, her minimum interbirth interval is 3–4 years.
- 4) The white-handed gibbon GM did not give birth until after 50–51 months of observation. Her minimum interbirth interval thus exceeds 4–5 years.

DISCUSSION

Interbirth Intervals

Field data suggest that interbirth intervals in wild *Hylobates lar* vary considerably. The 22- and 31-month interbirth intervals of AY are considerably shorter than the only other reported interval— 10 years—for a wild female monitored by Chivers and Raemaekers (1980). GM showed a moderately long estimated minimum interval of 4–5 years. In captivity, interbirth intervals of *H. lar* generally approximate 3 years (Table III), but under certain breeding regimes, the mean interval may be as low as 9 months (Kawakami and Kollias, 1984).

Fewer data are available for *Hylobates syndactylus*. A wild female at Kuala Lompat, Malaysia gave birth to three surviving offspring at intervals of 4 and 6 years (Table III). Minimum interbirth intervals for all three wild females at Ketambe also surpassed 3 years. Hill (1967) reported a much shorter interbirth interval of 9 months for a captive, but it is not clear

Table III. Intervals Between Successful Births in *Hylobates syndactylus* and *Hylobates lar*^a.

Female	Context	Interbirth Interval (yr) ^b	Source
<i>Hylobates syndactylus</i>			
Murgatroyd	Wild	4	Chivers & Raemaekers (1980)
		6	
Unnamed 1	Captive	0.7	Hill (1967)
Unnamed 2	Captive	2.5	Hill (1967)
PN	Wild	>3-4	This study
CJ	Wild	>3	This study
CO	Wild	>3.4	This study
<i>Hylobates lar</i>			
Gertie	Wild	10	Chivers & Raemaekers (1980) ^c
AY	Wild	1.8	This study
		2.6	
Unnamed	Captive	3.1 ± 1.3 ^d	Crandall (1964)
Unnamed	Captive	3.3 ± 1.7 ^e	Haggard (1965); Lancaster (1966)
GM	Wild	> 4.2	This study

^a"Interbirth interval" here refers to the period between births of live infants which did not die within a few months of birth.

^bInterbirth intervals with a greater sign indicate minimum estimated birth intervals for parous females (see text); intervals without the sign are directly observed interbirth intervals.

^cChivers and Raemaekers (1980) did not observe the first of the two births defining this interval, but as this first infant was "only a few months old" and carried by the adult female when their study began, the interbirth interval they provide is most likely accurate.

^dRange, 2.4-5.8 years ($N=5$ intervals).

^eRange, 1.8-6.8 years ($N=6$ intervals).

whether this interval was artificially shortened by the management practice of infant removal for hand-rearing, which typically accelerates resumption of cycling in the mother (Kollias and Kawakami, 1984; Williams, 1986).

The small number of cases implies that interbirth intervals for wild siamang and white-handed gibbons are quite variable and may often exceed—sometimes considerably—the oft cited 2- or 3-year period. Observations for wild siamang at Kuala Lompat and Ketambe suggest interbirth intervals typically exceeding 3 years. This may apply generally to white-handed gibbons too, since both extremely short and long intervals have been reported at the two study sites. That conclusion is further supported by a minimum interbirth interval of 3.2 years observed for the closely related (to *H. lar*) species, *Hylobates agilis* (Mitani, 1990). Interbirth intervals of such length are comparable to those reported for pongids: *Gorilla gorilla* and *Pan troglodytes* (Galdikas and Wood, 1990). This conclusion

has implications for understanding reproductive potential and variance in female reproductive success.

Reproductive Potential

The interaction of three biological parameters determines the reproductive potential of females: longevity, age at sexual maturity, and interbirth interval. Carpenter (1940) first suggested that the reproductive potential of a white-handed gibbon female was 10 offspring, a figure derived by assuming a life span of 30 years, puberty at 8–10 years, and an interbirth interval of 2 years. The Ketambe data for female reproduction permit a reevaluation of these variables in the two study species. Our current knowledge of maturation and longevity comes primarily from captivity.

Sexual Maturity. Ellefson (1974) suggested that wild white-handed gibbons become sexually mature at the age of 6 years in contrast to the 8–10 years first proposed by Carpenter (1940) on the basis of his observations of menarche in a captive individual. Geissmann (1991) suggests that female white-handed gibbons in captivity are 6–9 years old at the time of their first births, but he emphasizes that in most published reports age is estimated rather than known precisely by observers. Sexual maturity at 8–10 years for *H. lar* corresponds with the age generally suggested for social maturity i.e., emigration from the natal group or acquisition of first mates (Chivers and Gittins, 1978; Gittins and Raemaekers, 1980).

Given the association between body size and age at sexual maturity common among eutherian mammals (Calder, 1984; Harvey and Clutton-Brock, 1985), a slightly later, or at least equivalent, age at sexual maturity is expected for the larger siamang. Chivers (1972, p. 125) suggested that a wild siamang “appears to be sexually mature” soon after 5 years of age, but another 3 or 4 years may elapse before emigration and pair formation (Chivers, 1974). Estimates of age at first birth from captivity generally suggest 8–10 years for *H. syndactylus*, though a female only 5.2 years old gave birth to a live infant (Geissmann, 1991).

Thus, in general accordance with Carpenter’s analysis, sexual maturity may still be reckoned as occurring around 8–10 years. Nevertheless, this age may not always correspond with the onset of the reproductive career, as Carpenter (1940) surmised.

Longevity. The only data concerning longevity of wild siamang and white-handed gibbons are deductions derived from the assumed ages of individuals at the beginning of a study and the duration of subsequent observation. The “oldest” of these wild hylobatids is an adult female siamang monitored for about 10 years, suggesting an age of 18–20 years; Chivers

and Raemaekers's (1980) and Bennett and co-workers' (1983) speculations that she was actually 25–28 years old are based on the assumed maternity of the subadult male of her group at the beginning of the study, which is an assumption that observations at Ketambe suggest may sometimes be unreliable (Palombit, 1994a).

The maximum lifespan for a captive white-handed gibbon—31 years, 7 months (Jones, 1968)—has been used since Carpenter (1940) as a rough approximation of typical longevity in the wild. Gibbons in at least two other zoos have also approached this life span (Haggard, 1965) and are apparently still capable of reproducing (Lancaster, 1966). The maximum longevity recorded for captive siamang exceeds 20 years (Nowak and Paradiso, 1983), but Crandall (1964) suggests that survival past 14 years is noteworthy. A lower life expectancy in siamang would be somewhat surprising given their larger size (Harvey and Clutton-Brock, 1985), but the apparent difference cannot be attributed simply to sampling error since populations of captive siamang and white-handed gibbon are quite large (Mootnick, 1984; Fox, 1984). In light of the pronounced variation in survivorship and the generally low viability of hylobatids in captivity (Crandall, 1964), it is uncertain whether a 30-year zoo longevity should be viewed as an unusual prolongation of life or as an accurate reflection of wild life spans artificially abbreviated by captivity. Thus, although I reject the 30- to 40-year life span suggested originally by Carpenter (1940), I adopt the conventional 20- to 30-year life span (Gittins and Raemaekers, 1980; Leighton, 1987) while noting that the generality of this figure and its implicit uniformity within the Hylobatidae have yet to receive empirical verification from the wild.

The current data on sexual maturation and longevity thus yield a female reproductive lifetime of approximately 10–20 years, though the upper end of this range is generally used in estimates (Carpenter, 1940; Harvey *et al.*, 1987).

Given that the Ketambe data suggest interbirth intervals >2–3 years and that normal longevity may be shorter than the >30-year captive record, the reproductive potential of white-handed gibbons and siamang may be <10 offspring. Moreover, although I accept Carpenter's original estimate of age at menarche, sexual maturity may not coincide with the actual initiation of reproduction. Young adults may not obtain their first mates until well after attainment of sexual maturity. For example, the subadult female AA of this study was still unmated > 4 years after emigration from her group and apparent menarche based on onset of labial eversions. This may further reduce the length of a female's reproductive career.

Pregnancy termination and early postpartum infant death also decrease the total expected reproductive output by increasing the interval

between successful births, i.e., infants that survive to weaning. Such reproductive failure is well documented in mammals (Wasser and Barash, 1983), but I am first to report it—in the form of infant abandonment, stillbirth, and possible abortion—among wild hylobatids. Stillbirths, abortions (as late as 5 months into pregnancy), premature births, and early postpartum death are common among captive *Hylobates syndactylus* and *H. lar* (Crandall, 1964; Haggard, 1965; Hill, 1967; Breznock *et al.*, 1977; Kawakami and Kollias, 1984; Geissmann, 1991). For example, in one breeding colony of 14 wild-born white-handed gibbons, approximately 64% of first births were stillborn among primiparous females that subsequently had live births, while 86% of all females had at least one failed pregnancy and 14% experienced two failed pregnancies over a period of 5.5 years (Kawakami and Kollias, 1984; Kollias and Kawakami, 1984). Among siamang in zoos, 20% of newborn infants were stillborn or died within 24 hr (Geissmann, 1991). Aspects of captivity or breeding programs may disturb female reproduction, but abortions and stillbirths sometimes have biological causes that are possible in the wild, such as bacterial infection (Breznock *et al.*, 1977). At Ketambe, three of the four wild females that were adult at the beginning of the study experienced at least one episode of reproductive failure during 6 years.

Reproductive failure in the form of abandonment of infants as old as 6 months occurs in captive *Hylobates syndactylus* and *H. lar* (Rumbaugh, 1967; Breznock *et al.*, 1979; Kawakami and Kollias, 1984) and *H. pileatus* (Badham, 1967). Like captive gibbon females that rejected infants because mammary gland lesions hindered nursing (Kawakami and Kollias, 1984), the siamang abandonment at Ketambe occurred in the context of impaired maternal ability to provide care.

The Ketambe data suggest that reproductive failure via pregnancy termination and neonatal abandonment is not simply an artifact of captivity. It may reflect a female strategy to discontinue reproduction under socially or ecologically unfavorable conditions (Wasser and Barash, 1983; Mori and Dunbar, 1985; Hrdy, 1986). An intriguing example is the apparent termination of the pregnancy of the adult white-handed gibbon GM. This was coincident with the initiation of pair formation with a new male to replace her deceased former mate (Palombit, 1994a), which suggests the possibility of pregnancy block or the Bruce effect (Bruce, 1961; Huck, 1984).

Finally, mortality among juveniles and subadults is likely to reduce reproductive success in white-handed gibbons and siamang further, though the scarcity of relevant, longitudinal data limit quantitative estimation of this effect. Mitani (1990) reports a juvenile mortality rate of 18% in *H. agilis*, a close relative of *H. lar*. There are few field data on the survivorship of dispersing subadults, but it is likely that they suffer an extremely high mortality given the rarity of suitable breeding sites in typically saturated

habitats (Leighton, 1987; Mitani, 1990). High mortality rates may be mitigated to some extent by parental assistance in founding a new territory (Tilson, 1981) or mate acquisition through replacement of a paired adult of the same sex in an already established group (Palombit, 1994a).

Thus, the actual reproductive potential of siamang and white-handed gibbon females would appear to be considerably less than the 10 offspring first suggested for the latter by Carpenter (1940). A definitive description of reproduction in these species requires observation of many more individuals over more years than are encompassed by the data presented here. Ideally, the lifetime breeding success of females should be described. Although the few and highly variable data currently available on interbirth intervals complicate a reestimation of the reproductive potential in *H. lar* and *H. syndactylus*, they appear to warrant an estimated average of only approximately five offspring in a female's lifetime. This reproductive potential is low relative to other catarrhines but comparable to that suggested for *H. klossii* on the Mentawai Islands (Tilson, 1981) and for some great apes—*Pan troglodytes* (Tutin, 1979; Ghiglieri, 1987; Nishida *et al.*, 1990).

Variance in Female Reproductive Success

Taken together, the data for *Hylobates lar* and *H. syndactylus* from Kuala Lompat and Ketambe imply substantial variation in interbirth intervals among females and, hence, in female reproductive success. Reproductive rate is not the only component of a female's reproductive success, but information is currently too limited to include other relevant variables, such as the length of female reproductive lifetime and the survivorship of *known* offspring in the wild. Pronounced variation in female breeding success in white-handed gibbons and siamang contrasts with theoretical predictions of low variance in reproduction among female mammals, particularly in monogamous mating systems (Trivers, 1972; Emlen and Oring, 1977). But this result is consistent with recent longitudinal data indicating greater than expected variance in female mating success among polygynous mammals (Clutton-Brock, 1988b).

Potential sources of differential reproductive success in female white-handed gibbons and siamang are unclear. Pair bond stability, food supply, and male parental care have all been offered as important determinants of variation in female fecundity in monogamous animals in general (Kleiman, 1977; Barlow, 1988) and in gibbons in particular (Brockelman *et al.*, 1974; Gittins and Raemaekers, 1980). The number of white-handed gibbon and siamang females for which reproductive histories are available is too few to permit a detailed analysis of the possible influences of these factors.

The possible importance of pair-bond stability is implicated by the fact that the female with the shortest interbirth intervals at Ketambe—the white-handed gibbon AY—was the one that remained paired to the same male throughout the entire 6-year observation period (Palombit, 1994a). Increased food supply may also have contributed to her relatively high rate of reproduction: as a result of the eventual disease-induced dissolution of two siamang study groups (Palombit, 1992), all siamang competitors were absent from white-handed gibbon Group A's territory from late 1987 through 1991. Given the high degree of dietary overlap between them (Raemaekers, 1979; Palombit, 1992) and the siamang habit of displacing and harassing white-handed gibbons feeding in shared fruit patches (Raemaekers, 1978a,b, 1984; Brockelman and Srikosamatara, 1984)—which is particularly pronounced among Sumatran subspecies (MacKinnon, 1974, 1977)—it is possible that Group A experienced a significant increase in its effective resource base since early 1988, which may have compressed the interbirth intervals of AY. This disappearance of siamang may not have similarly affected the reproduction of the other parous white-handed gibbon (GM), since her mating status remained unstable during much of this time as she slowly acquired a new mate after the death of her former mate (Palombit, 1994a).

Variation in direct paternal care may influence female reproduction in siamang, in which males are known to carry infants during their second year of life (Chivers, 1974; Fox, 1972; Alberts, 1987; Dielentheis *et al.*, 1991; Fischer and Geissmann, 1990). A male siamang that provides this care may enhance the reproductive success of his mate, possibly by increasing infant survivorship or by reducing interbirth intervals of the female (Kleiman and Malcolm, 1981; Anderson, 1992), which is spared the typically high energetic costs of infant-carrying (Altmann and Samuels, 1992).

During my study, only one male siamang resided in the same group as a yearling infant and therefore had the opportunity to exhibit infant carrying. This male did not provide such care (Palombit, 1992), which may have lengthened the interbirth interval of his mate (PN). Although she did not continue to carry the infant, the possibly related replacement of her noncaring mate by another male may have postponed her next pregnancy (Palombit, 1992, 1994a). This correlation must be treated as tentative, however, for not only is there no empirical evidence that paternal care in siamang affects female reproductive rate, but recent studies have shown that the pronounced, direct parental investment of males in some monogamous birds often fails to improve female reproductive success significantly (Gowaty, 1983) or does so only under ecologically poor conditions (Bart and Tornes, 1989).

Greater variance in female mating success may have implications regarding the sexual and social behavior of adults. Long-term studies of avian monogamy suggest that the quality of an individual's mate may be an important determinant of breeding success (Clutton-Brock, 1988b). If this is also the case for white-handed gibbons and siamang, then substantial variance in female reproductive success suggests that females (and males) may be under strong selection to exert mate choice through mate-switching or extra-pair copulations. There is growing behavioral evidence that mate replacement via abandonment of a partner or incitement of a mate's desertion as well as extra-pair copulations may be more common than heretofore appreciated in white-handed gibbons and siamang (Palombit, 1994a, Reichard, 1994) and possibly in hylobatids in general. Dahl and Nadler (1989, 1992) have also argued that the anatomical structure and cyclical changes of the external genitalia of the female white-handed gibbon are unusual for a monogamous primate and suggestive of some function related to mate choice via retention of and switching partners.

The criteria females might use in choosing mates are not clear but may include male ability or propensity to contribute directly to parental care in siamang and territorial defense in both species (Chivers, 1974; Ellefson, 1968, 1974; Leighton, 1987; Raemaekers and Raemaekers, 1985). Natural variation in these male behaviors and how they affect female reproductive effort are not known. How mate choice might operate in extra-pair copulations is equally obscure. There may be genetic benefits (McKinney *et al.*, 1984; Westneat *et al.*, 1990; Birkhead and Møller, 1992; Wagner, 1992), but extra-pair copulations may involve related, but nongenetic benefits, such as allowing a female to appraise the receptivity or availability of potential (future) mates in neighboring groups (*sensu* Colwell and Oring, 1989; Wagner, 1991) and to facilitate the establishment of a new pair bond if mate-switching becomes possible. Conversely, extra-pair copulations may not reflect mate choice *per se*, but may, for example, be a female tactic to reduce the overall costs of territorial defense against neighboring groups by lowering intersexual aggression from males during intergroup interactions. Like females, paired monogamous males are expected constantly to assess mate quality in light of current reproductive opportunities. Given that high variance in reproductive success in females establishes a context in which they may benefit from extrapair copulations, males may further engage in mate-guarding tactics that discourage such sexual behavior. This may be reflected in male social behaviors. For example, in spite of apparent differences in the nature of siamang and white-handed gibbon pair bonds, males of both species appear more active than females in maintaining proximity to the pair mate (Palombit, 1992) and in interacting aggressively with conspecific neighbors during intergroup

encounters (Ellefsen, 1968; Chivers, 1974). In *H. lar*, a group containing a sexually receptive female is less likely to interact with neighboring groups (Ellefsen, 1974), though it is not clear whether this is due to male initiative.

More research is needed to refine estimates of variance in female reproductive success and to clarify the generality, proximate causes, and reproductive correlates of stable versus dynamic patterns in pair bonds. Is the long-term stability of some pair bonds (Mitani, 1990) due to the advantages such bonds confer to the participants or to the limited opportunities to acquire and change mates (*sensu* Freed, 1987; Marzluff and Balda, 1988; Davies, 1991)? The spatiotemporal availability of opportunities for adults to differentiate among and to acquire mates may ultimately be one of the most important determinants of variation in female mating success in white-handed gibbons and siamang.

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