

Home-Range Characteristics and the Influence of Seasonality on Female Reproduction in White-Handed Gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand

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ABSTRACT A three-year (2001–2003) study was carried out on the home range characteristics of seven wild white-handed gibbon (*Hylobates lar*) groups focusing on the spatio-temporal distribution of food resources at Khao Yai National Park in northeastern Thailand. These results were combined with 23 years (1980–2003) of reproductive performance data on seven females from the same focal groups. Reproductive performance was equal among females with regard to birth, weaning and maturation ratios, and independent of variation in food availability. Offspring mortality, however, was significantly positively correlated with home-range size. In addition, there was an increase in offspring mortality just after weaning, suggesting that the increase in the daily dis-

tance traveled by juveniles contributed to this mortality. Conceptions clustered during the first half of the year when food production was at its peak, which presumably allowed females to accumulate sufficient body reserves to resume ovarian cycling. Our results place Khao Yai gibbons closer to Cercopithecidae than great apes in terms of the temporal pattern of reproductive events, though gestation, lactation, inter-birth interval, and offspring maturation are considerably longer in gibbons, placing them closer to the other apes. Our findings underline the unique phylogenetic position of these small-bodied apes in terms of reproductive patterns in primates. *Am J Phys Anthropol* 135:1–12, 2008. © 2007 Wiley-Liss, Inc.

Primates, like other mammals, have evolved a reproductive physiology that demands great female investment for each single reproductive event. Physiological activities of early reproductive phases, like regular cycling, gestating, and nursing, place females under substantial energetic pressure and require a constant and high input of nutritional resources (Lee and Bowman, 1995). Female reproductive success is initially limited by the number of eggs developed to ovulation, followed by the number of offspring born alive and nursed to weaning, and eventually by all post-weaning investment still necessary to support an offspring to the onset of its own reproduction. Access to food resources plays a critical role for females because under sub-optimal nutritional conditions reproduction may be delayed or temporarily ceased (Lee, 1987; Clutton-Brock, 1989). Nutrients essential for reproduction are primarily acquired through feeding, which is normally a direct reflection of the quality of an animal's immediate environment. Females living in relatively poor habitats may have lower reproductive success because of lower energy intake. An example of this relationship is found in red deer hinds (*Cervus elaphus*), where hinds grazing in areas with higher grass quality showed significantly higher lifetime reproductive success than hinds grazing on nitrogen-poor soils (Iason et al., 1986). Other work has also confirmed a direct link between a females access to resources and her reproductive

performance (Kenagy and Bartholomew, 1985; Martin, 1987; Bolton et al., 1992).

Because of the influence of food availability on female reproductive success, natural selection favors females that tend to reproduce during favorable periods of the year. This timing is more likely to increase reproductive output, survival of offspring, and future reproductive attempts (Lancaster and Lee, 1965). Seasonal reproduction is expected in species living in habitats that show predictable patterns of variation in food availability and in species that are relatively small in body size (van Schaik and van Noordwijk, 1985; Di Bitetti and Janson, 2000). Subtropical forests, where most primates live,

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often show significant seasonal variation in food availability (Wright and Cornejo, 1990; Peres, 1994), which may lead to clear seasonality in births, conceptions, and weaning (Butynski, 1988; Di Bitetti and Janson, 2000; Borries et al., 2001). However, additional factors, such as weather (De la Torre et al., 1995) or photoperiod variation (Rasmussen 1985; Welker et al., 1987; Fernandez-Duque et al., 2002), have been reported to cause seasonality in reproduction.

Reproductive seasonality has been demonstrated in several primate species and variation in food availability may influence different stages of the reproductive cycle (Di Bitetti and Janson, 2000). In some seasonally breeding catarrhine primates, for example, a distinct annual or biannual reproductive cycle has evolved (Ardito, 1976; Rowe, 1996), which may allow mating as well as the end of lactation to take place when food is abundant. However, when either births and lactation or conceptions coincide with periods of high food availability, two distinct scenarios have been reported that suggest different evolutionary explanations.

In New World primates, a typical reproductive pattern is the clustering of births just prior to forest productivity peaks (Di Bitetti and Janson, 2000; tamarins, Goldizen et al., 1988; *Alouatta*, Thorington et al., 1984; Rumiz, 1990). Goldizen et al. (1988) proposed that the timing of births corresponds to the greatest energetic demands of females during peak lactation and when food availability is the highest. During the lactation process, the energetic stress on a female increases as an infant develops until the infant begins to ingest solid food. As the infant becomes more independent the mother's energetic investment starts to decline until the infant is eventually weaned. Nievergelt and Martin (1999) found that for *Callithrix jacchus* the highest energy need was near peak lactation, defined as the time when an infant's demand for milk is greatest and before milk is supplemented with solid food. Di Bitetti and Janson (2000) have confirmed this interpretation for small-bodied primates, whereas for larger bodied neotropical primates they found a synchronization of weaning with peaks in food availability.

In Nepalese Hanuman langurs (*Semnopithecus entellus*), births were concentrated during the dry season when food availability was low and the physical condition of females was poorest. This suggests that energetic demands in late gestation and early lactation were not responsible for reproductive seasonality. Instead, seasonality in reproduction appeared to be a consequence of the fact that conceptions peaked when a female's physical condition was at its best and food availability was at its highest (Koenig et al., 1997). This pattern appears to be typical of Old World primates as noted in *Macaca fuscata* (Takahashi, 2002), *Macaca fascicularis* (van Schaik and van Noordwijk, 1985), and *Theropithecus gelada* (Dunbar, 1984). In these cases, the majority of females conceived only after they accumulated sufficient fat reserves to meet the physiological demands of ovulation (Bercovitch and Strum, 1993). The same relationship between food availability and conception has been found in the nonseasonally breeding Gilgil baboon (Bercovitch and Harding, 1993), in *Erythrocebus patas*, *Cercopithecus aethiops tantalus* (Nakagawa, 2000), and in one large New World primate, *Alouatta caraya* (Rumiz, 1990), highlighting the high energetic demands required prior to conception (Bercovitch, 1987).

In contrast to small-bodied monkeys, great apes are considered as nonseasonal breeders (*Pan troglodytes*:

Boesch and Boesch-Achermann, 2000; *Pan paniscus*: Furuichi et al., 1998; *Gorilla beringei*: Watts, 1998), because they depend less on immediate resource levels due to a larger body size and lesser seasonality of their habitats. Nevertheless, in some great ape populations, seasonal reproduction has been documented. In Gombe chimpanzees more births were observed at the beginning of the rainy season, during a period of relatively lower resource productivity in the forest. Consequently, conceptions occurred more often in the dry season when food productivity was estimated to be higher; the relationship was not tested directly because food productivity was only defined indirectly (Wallis, 1997). Patterns suggesting seasonal breeding were likewise reported for Mahale chimpanzees, where swellings were seen more often during the rainy season when food productivity was highest (Nishida et al., 1990). In orangutans (*Pongo* sp.), conceptions appeared to be stimulated by high food availability as indicated by high levels of estrone conjugates in the urine of nonpregnant females; these levels dropped considerably during low-quality/low-food availability periods (Knott, 2001). In humans, extremely harsh environmental conditions can also result in seasonal reproduction. Among nomadic Turkana women, the highest conception rates coincided with the early dry season when food supplies were highest and the women had also reached their highest nutritional status (Leslie and Fry, 1989).

Gibbons are interesting apes to study in terms of seasonality in reproduction because of their small body size, which resembles the body sizes of many monkeys more so than other apes. It is important to note, though, that despite their smaller body size, gibbon life history traits and brain size resemble patterns more comparable to the other apes. Evolutionary links between body size, life history, and intelligence in primates is still unclear (cf. Gebo, 2004), but it has been suggested that body size and brain size co-evolved (Ward et al., 2004). This suggestion puts gibbons in an interesting position because the increase in brain size in gibbons was apparently not intimately coupled with an increase in body size. Little is currently known thus far about both the cognitive capacities of gibbons and the effects of small body size on reproduction in a relatively large-brained primate.

The purpose of this study is to investigate how variation in home range productivity influenced reproductive timing and reproductive success of seven gibbon females. We first investigated the hypothesis that reproduction in gibbons is seasonal. Gibbons are of relatively small body size (Groves, 1972; Smith and Jungers, 1997) and more closely resemble Cercopithecidae monkeys than great apes, and therefore have great similarities in their reproductive biology. To test our hypothesis, we predicted there to be a positive relationship between the timing of conception and food availability, with more conceptions occurring during periods of high forest productivity. We also investigated a second hypothesis that females inhabiting higher-quality home-ranges would obtain greater reproductive success than females inhabiting lower-quality ranges, as female reproduction is assumed to be predominantly constrained by access to food resources. To test this hypothesis, we predicted that: a) birth rates of females in high-quality ranges would exceed birth rates of females living in lower-quality ranges, because access to more food is expected to shorten the time between consecutive births; b) weaning rates of females living in high-quality home-ranges would be shorter than those of females living in lower-quality

TABLE 1. Offspring used in the evaluation of female reproductive performance and seasonality in reproduction

Group	Offspring	Abbreviation	Birth month	±	Conception month	Lactation peak
A	Actionbaby	Acti.	Oct 80	1 m		Low precision
	A2mD	A2mD	—	—	—	—
	Amadeus	Amad.	Oct 87	1 m		Low precision
	Aran	Aran	—	—	—	—
B	Akira	Akir.	Oct 93	1 d	Mar 93	Nov 93
	Britt	Brit.	—	—	—	—
	Brenda	Bren.	Nov 87	5 m		Low precision
	Benedetta	Bene.	—	—	—	—
C	Bua	Bua	Nov 97	6 d	Apr 97	Dec 97
	Chet	Chet	Nov 83			Low precision
	Christopher	Chri.	Des 86	3 m		Low precision
	Caleb	Cale.	—	—	—	—
D	Cyvana	Cyra.	Nov 93	1 w	Apr 93	Dec 93
	Chikyu	Chik.	Nov 96	1 d	Apr 96	Dec 96
	Chuu	Chuu	Sep 99	2 d	Feb 99	Oct 99
	Chumpon	Chum.	Sep 02	0 d	Feb 02	Oct 02
	Dae	Dae	Oct 91	6 m		Low precision
	Dara	Dara	Oct 95	1 m		Low precision
	Dino	Dino	Feb 98	1.5 m		Low precision
H	Dodo	Dodo	Nov 00	2 m		Low precision
	Dingo	Ding.	Oct 03	1 w	Mar 03	Nov 03
	Hank	Hank	—	—	—	—
	Haley	Hale.	Oct 92	1 w	Mar 92	Nov 02
R	Hima	Hima	Oct 95	1 m		Low precision
	Hom	Hom	Aug 98	1 m		Low precision
	Henry	Henr.	Aug 01	3 d	Jan 01	Sep 01
	Rooster	Roos.	Oct 93	2 w	Mar 93	Nov 94
	Rung	Rung	Oct 96	2 d	Mar 96	Nov 96
T	Rio	Rio	Sep 99	2 d	Feb 99	Oct 99
	Rak	Rak	Jan 02	1 d	Jun 01	Feb 02
	Tarzan	Tarz.	Aug 00	0 d	Jan 99	Sep 00
	Thala	Thal.	Jul 02	4 d	Dec 01	Aug 02

ranges, because more food resources allow females to wean offspring faster; and c) maturation rates of offspring would be faster on high-quality home-ranges, as better resources are expected to allow faster development.

METHODS

Study site and animals

The study was conducted between June 2001 and May 2003 at the Central Mo Singto site, Khao Yai National Park, Thailand (2,168 km²; 101°22' E, 14°26' N; ~130 km NE of Bangkok), in slightly hilly terrain 730–890 m above sea level. The Central Mo Singto site covered approximately 2 km² and was inhabited by a large population of white-handed gibbons (*Hylobates lar*) that have been studied since the late 1970s (see Raemaekers and Raemaekers 1985; Reichard and Sommer 1994, 1997; Reichard 1995; 1998, 2003; Bartlett, 1997; Brockelman et al., 1998). Seven groups (named A, B, C, D, H, R, and T) were the focus of the present study; the seven resident females did not change during the study period (see Table 1 for details).

Khao Yai is largely a seasonally wet, evergreen forest (Kerby et al., 2000; Kitamura et al., 2004a). It experiences a distinct dry season (November–April) and wet season (May–October). Data collected on forest productivity (plant phenology data) from February 2001 to September 2003 documented an average precipitation of 2,697 mm (range 2,976–2,297 mm), which closely corresponded to rainfall records of other researchers at the site during the years 1993–2001: 2,326 mm (Kitamura et al., 2004b); 1993: 2,030 mm (Poonswad et al., 1998);

1994: 2,695 mm (Bartlett, 1999); and 2004: 2,127 mm (Kanwatanakid-Savini, unpublished data). Average daily temperature varied annually between 18.7 and 28.3°C, and mean humidity ranged from 64.6% during the dry season to 77.1% during the wet season.

Measures of home-range size

Maps of the home-ranges for each study group were produced from daily night-tree to night-tree travel route maps. Travel data were collected by the authors and field assistants of the Khao Yai gibbon long-term research project by continuously transcribing the movements of observed groups on, and with reference to, a detailed trail map. A traverse measured trail system follows along natural landmarks such as ridges and elephant tracks. Trails were rarely farther apart than 50 m, and most trails were as close as 30 m or less. Trails were marked at 25 or 50 m intervals, which allowed us to precisely map individuals' travel paths. Observed travel routes were digitized in ARC/INFO 3.4; the lengths of the routes were measured using ArcView 3.0a software. Day journey records varied between study groups (A, $n = 117$ days; B, $n = 98$ days; C, $n = 130$ days; D, $n = 86$ days; H, $n = 135$ days; R, $n = 116$ days; and T, $n = 137$ days). Day journey records were collected by the authors and included information from a long-term database between May 2001 and December 2003. The size and shape of our study groups' home-ranges were unchanged since the groups were followed. Estimates of home-range sizes were based on all observed travel routes using the minimum convex polygon method (see White et al., 1996; Linnell et al., 2001). Minimum polygon outlines were

then digitised in ARC/INFO 3.4, and the areas of the polygons were calculated using ArcView 3.0a software to obtain the actual home-range sizes.

Forest food productivity cycles and spatial distribution of resources

The spatial distribution of plant resources was measured on 13 north-south transects (total length 19.4 km, ranging from 620 to 2,100 m) across the same seven gibbon home-ranges. A preliminary study of group A's home-range, in which nearly all fruiting trees had been identified and mapped, indicated that sampling 20% of the home-range could provide a reliable estimate of forest structure and botanical composition of the entire home-range. Thus, our study transects included 20% of each of the study groups' home-ranges covering a total of 39.8 ha. Along transects, trees larger than 10 cm DBH were marked, measured, and the species was identified. A total of 19,524 individual trees were included in our analyses.

To quantify the gibbons' diet, the relative time different plant species were consumed by gibbons over the total time spent feeding was measured. Plant species consumed were ranked from highest to lowest in terms of their contribution to the total foraging time. Because our aim was to understand the effects of variation in ecological quality of home-ranges, we were less interested in the overall diet of gibbons and more interested in knowing which plant species were of greatest importance to the gibbons. We therefore assembled a monthly ranking list where the species with the highest score of feeding time was entered at the top of the list. To this top species, the second highest scoring species was added below, and below this, the third highest scoring species was added. This process was continued until cumulatively 80% of the gibbons' feeding time had been documented. Plant species that appeared on the list were considered an important food species in the gibbons' diet. Lists of important food species varied between months according to availability as well as to the gibbons' feeding requirements and priorities. Important gibbon food species were identified on a monthly basis by direct feeding observations of five gibbon groups (A, C, H, R, and T) from July 2001 to March 2003. All plant species that were considered important across months were included in our phenological monitoring (see later). On average, 9 ± 2.8 species (SD) were considered important in any given month, and in total, important species included 22 fig species and 26 non-fig species. Systematic plant productivity monitoring initiated in May 2001 did not originally focus on all of the species identified as important gibbon food species because it was based on past knowledge of gibbon diets, eventually with greater knowledge of key food species for gibbons, monitoring did include all important species. Each gibbon group was observed for a minimum of 5 days per month by two trained field assistants. Data on feeding activities were collected by continuous observation from night-tree to night-tree (cf. Martin and Bateson, 1993), alternating every hour between males and females. Food sources were known by the observers or were later identified from collected plant samples.

During phenology walks, which started in May 2001 and ended in September 2003, 10 individual trees of each important non-fig tree species were monitored once a month for the presence of ripe and unripe fruits, young leaves, flowers, shoots, and buds. Abundance was esti-

mated on a relative 0–4 point scale, with 0 representing the absence of a given plant part and 4 scoring the full presence of a crown. All figs observed in the study site were monitored twice a month because reproductive cycles of some fig species were expected to be shorter than a month (cf. Poonswad et al., 1998).

Home-range quality

Home-range quality was defined as the monthly productivity per hectare in each home-range. Our productivity measures combined the measure of food abundance (FAI) with a biomass coefficient (b), which included relative fruit load (see below). FAI was measured monthly for each of the seven separate home-ranges by applying a food abundance index (cf. Andersen et al., 2002; Mitani et al., 2002), which included data on each important food species [Eq. (1)].

$$\text{Food Abundance Index [FAI]} = \sum_{k=1}^n D_k B_k P_{km} \quad (1)$$

Where D_k is the density of species k in the home-range (stems/hectare), B_k is the mean basal area of species k in each home-range ($\text{cm}^2/\text{hectare}$), and P_{km} is the percentage of observed trees of species (k) that produce ripe fruit in a given month (m). To obtain a productivity measure we multiplied the FAI value by the weight of fruit (b) in kilograms per cubic meter of tree canopy for each species at the peak of fruiting [Eq. (2)] (modified after Direnstein, 1986)

$$\text{Productivity index} = \text{FAI} * b \quad (2)$$

The weight of the fruit was estimated by multiplying the weight of a single fruit of a given species by the estimated number in a cubic meter of the crowns at the species' productivity peak, giving maximum fruit production. The number of fruits in a cubic meter was scored in categories starting at 10 and increasing to 25, 50, 100, 250, 500, 1,000, and so on. The value was obtained after visual examination of a randomly selected (and estimated) cubic meter of the crown (cf. Gautier-Hion and Michaloud, 1989). The equation used the basal area included in the FAI equation as an approximate value for crown volume (Chapman et al., 1992). Finally, months of high and low productivity, defined as those exceeding twice the standard deviation from the average productivity across the entire productivity period, were measured.

Measures of female reproductive performances

Long-term demographic data of seven females were collected by monitoring the presence or absence of group members during annual surveys and by using behavioral observations taken for other purposes. We subdivided data on female reproduction into three groups according to the precision of data, study intensity, and aim of analysis (see Table 2 for details). The first subset of data spanned 23 years and included all 25 records of observed births from October 1980 until October 2003. The data were used to calculate rates of offspring birth, weaning and maturation, and mortality. This subset included published records of births in study groups A, B, and C (Treesuon, 1984; Brockelman et al., 1998) gathered

TABLE 2. Summary of data-sets relative to female reproduction

Group	Observer	Start of social history record	Long-term female reproductive performance				Cohort life curve	Reproductive seasonality	
			Offspring born [n]	Weaned [n]	Matured [n]	Dead before maturation [n]	Offspring [n]	Start of precise birth record	Offspring born [n]
A	UT(1); WB(3); US/TB(1)	1980	5 Acti. A2mD Amad. Aran Akir.	5 Acti. A2mD Amad. Aran Akir.	3 Acti. Amad. Akir.	2 A2mD Aran	5 Acti. A2mD Amad. Aran Akir.	1993	1 Akir.
B	UR(3)	1991	2 Bene. Bua	2 Bene. Bua	1 Bren.	1 Bene.	3 Bren. Bene. Bua	1993	1 Bua
C	UR(5); FA(2)	1988	5 Cale. Cyra. Chik. Chuu Chum.	4 Cale. Cyra. Chik. Chuu	5 Chet. Chri. Cale. Cyra. Chik.	0	7 Chet. Chri. Cale. Cyra. Chik. Chuu Chum.	1993	4 Cyra. Chik. Chuu Chum.
D	UR(3); UR/TS(1); FA(2)	1997	3 Dino Dodo Ding.	2 Dara Dino	2 Dae Dara	2 Dino Ding.	5 Dae Dara Dino Dodo Ding.	1997	1 Ding.
H	UR(2); WB(1); TS/FA(1); CB/FA(1)	1992	4 Hale. Hima Hom. Henr.	4 Hale. Hima Hom. Henr.	2 Hale. Hima	2 Hank Hom	5 Hank Hale. Hima Hom. Henr.	1993	2 Hale. Henr.
R	UR(3); TS/FA(1); FA(1)	1992	4 Roos. Rung Rio Rak	3 Roos. Rung Rak	1 Roos.	1 Rio	4 Roos. Rung Rio Rak	1993	4 Roos. Rung Rio Rak
T	TS(1); FA(1)	1999	2 Tarz. Thal.	0	0	1 Tarz.	2 Tarz. Thal.	1999	2 Tarz. Thal.
Total			25	20	14	9	31		15

Female Britt was excluded from the cohort life curve calculation because she dispersed in 1991, and precise data on her were limited. A good social history record for group B started from 1991 onwards. Hence, the birth of female Brenda, which was known to have occurred some time in 1987 (see Table 1), was not included here.

prior to the onset of our own systematic monitoring early in 1990 (UR). The second subset of records included all 31 live births belonging to each studied female recorded between 1980 and 2003. This subset was used to construct the cohort life curve. Finally, the third subset comprised 15 birth records between 1993 and 2003 where we knew precisely the date of parturition, i.e. birth month (see Table 1). The latter data set was used to test seasonality of births.

We monitored reproductive females throughout the period included in our analyses (1993–2003) and added published birth records that had occurred before we began our monitoring program. Our observations of the Central Mo-Singto population exceed 3,000 contact hours with gibbons on more than 750 observation days between 1989 and 2003 (UR). We monitored the fate of all individual offspring used in our analyses except for A2mD.

Birth ratio was defined as the number of observed offspring ($n = 25$) born alive or carried, and known to belong to a given female over the years of observation (cf. Di Bitetti and Janson, 2001). The weaning ratio was defined as the number of fully weaned offspring observed ($n = 20$) over the years of observation (cf. Mann et al., 2000). Following Lee et al. (1991), it was assumed that peak lactation occurs around the time when infants

begin to consume solid food. In the Khao Yai population this period has been estimated to be about 4 weeks after birth (Treesucon, 1984; UR personal observation). This period was assumed for all infants in our sample, which suggested a lactation peak for females occurring about 1 month after birth (see Table 1).

Second, we investigated measurements (maturation ratio and mortality ratio) related to the survival of offspring. The maturation ratio was defined by the number of offspring that successfully reached physical maturity ($n = 14$) during the observation period (1980–2003). Physical maturity does not occur before 8 years of age in the Khao Yai population (Reichard, 2003). Because it was not possible to relocate dispersed animals, we could not use the actual age of first reproduction for offspring as age of maturation. We therefore calculated mortality ratios as the number of offspring deaths before reaching sexual maturity ($n = 9$) divided by the number of observation years (1980–2003). A cohort life curve was used to determine age-specific mortality of offspring (cf. Began and Mortimer, 1986). For this calculation we used our entire dataset (1980–2003) and included all infants in each observed group, including those that were already juveniles when the group was first monitored, except for one female, Britt ($n = 31$). Britt, a juvenile female from group B, was not included in the calculation of the

cohort curve because precise data available for her were relatively limited.

The inter-birth interval (IBI) is often used as an indicator of the relationship between female reproductive performance and habitat quality because it is assumed that better fed females can shorten their IBI and, consequently, increase their lifetime reproductive success (Clutton-Brock, 1988). We did not use this proxy because of our small sample size of precisely known consecutive births. Furthermore, lifetime reproductive success, which is highly variable among individuals (Clutton-Brock, 1988), and is directly correlated with habitat quality (Conradt et al., 1999), could not be included in measures of female reproductive performances because we lacked adequate data on the length of the reproductive lifetime of female gibbons.

Measures of seasonality in reproductive events

Following Lindburg (1987), we defined reproductive seasonality as “any tendency toward temporal clustering of reproductive activity, either discrete seasons or seasonal peaks”. Birth season was defined as “a discrete period of the year to which all births are confined. There must be some months during which no births occur” (cf. Lancaster and Lee, 1965). For the seasonality analyses, we considered the births we were certain of the parturition date (± 1 week) and when the births could be placed precisely within a given month. Following births, we back-calculated the date of conception. We used a value of 220 days of gestation in accordance with most published records suggesting 210 days gestation in captive white-handed gibbons (Hayssen et al., 1993) plus a 5% time increase as suggested by Borries et al. (2001) for wild primate populations.

Statistical analysis

Data on productivity variation for the entire area and for each home-range were analyzed by ANOVA, for which sphericity for repeated measurements was controlled. The relationship between female reproductive performances (birth ratio, weaning ratio, maturity ratio, and mortality ratio) and ecological variables (productivity/ha), as well as between seasonality in reproduction and ecological variables, was calculated using Pearson’s partial correlation tests after visual inspection of residuals indicated that assumptions for parametric statistics were not violated. When residuals did not fit the assumptions for parametric tests, we ran non-parametric Spearman rank correlations (Siegel, 1956). The relationship between

food seasonal variation and reproduction was tested using a paired sample *T*-test.

To establish whether there was a seasonal pattern in reproduction we used the Rayleigh test (Zar, 1999, p.622), which indicated whether the months when the majority of births were clustered differed significantly from the rest of the year. All tests were two-tailed with an α error level of 0.05. Productivity variation between groups was calculated using an ANOVA pair-wise comparison; for reproductive performance variation between females we used a one-way ANOVA. Statistical testing was run on SPSS release 11.0.

RESULTS

Productivity variation (seasonal and per group)

Over a period of two and a half years, average monthly variation in the food productivity index ranged from a maximum of 971 in April during the beginning of the rainy season, to a minimum of 147 in November and December during the beginning of the dry season (average = 451 ± 267 ; $n = 12$ “months”) (see Fig. 1). There were two peaks in forest productivity within a year, the first from January to April and the second from July to September. The second increase resulted from fruiting of a single species, *Choerospondias axillaris*. No significant difference was found among home-ranges in terms of productivity (repeated measurement ANOVA: $F_{(6,66)} = 2.01$, $P = 0.077$) (Table 3).

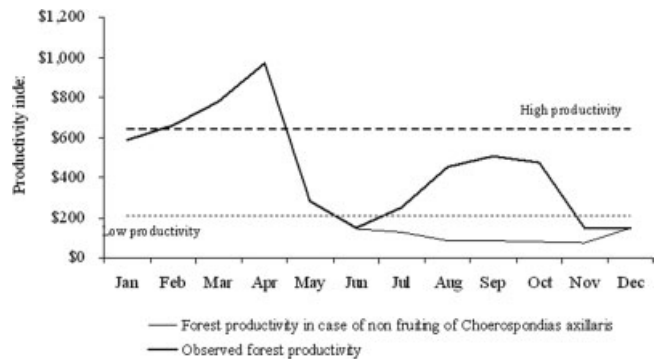


Fig. 1. Forest food productivity during the period of May 2001–September 2003. The presence of the second productivity peak (from July to October) is related almost entirely to the fruiting of *Choerospondias axillaries*.

TABLE 3. Home-rang size, daily travel distance, productivity, and female reproductive performance

	Group home range				Female reproductive performances			
	Size (ha)	Home range productivity index	SD (\pm)	Daily travel distance (m)	Birth ratio	Weaning ratio	Sexual maturity ratio	Mortality ratio
A	30.4	14,650	12,032	819	0.33	0.33	0.20	0.13
B	23.8	9,371	14,375	621	0.25	0.25	0.13	0.13
C	25.6	10,782	11,709	859	0.36	0.29	0.36	0.07
D	49.7	7,847	7,367	1,191	0.38	0.25	0.25	0.29
H	20.7	7,068	5,811	859	0.40	0.40	0.20	0.18
R	14.8	12,649	6,661	598	0.40	0.30	0.10	0.09
T	31.1	10,151	10,463	801	0.67	0.33	—	0.25
Between-group comparisons of female reproductive performance (One-way ANOVA)					$F_{(6,75)} = 0.079$ $P = 0.998$	$F_{(6,81)} = 0.318$ $P = 0.926$	$F_{(5,82)} = 0.694$ $P = 0.63$	$F_{(6,86)} = 0.478$ $P = 0.823$

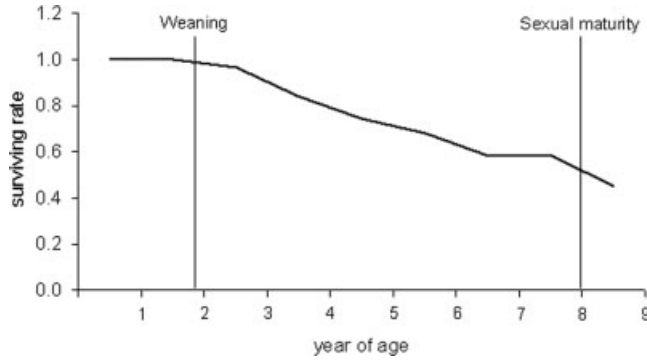


Fig. 2. Proportion of surviving offspring based on a cohort life table. In the Khao Yai gibbon population average weaning age was estimated at 22 months (Treesucon, 1984), while sexual maturity was estimated to be 8 years (Reichard, 2003).

Female reproductive performance and home-range quality

Female reproductive performance did not vary significantly across groups in terms of birth, weaning, achievement of sexual maturity in offspring, and death ratios (Table 3). The cohort life curve showed an increase in offspring mortality starting just after weaning at 24 months of age (Fig. 2). Overall, 45.2% of all offspring born since 1980 ($n = 31$) reached sexual maturity. The mortality ratio significantly correlated with home-range size ($R^2 = 0.597$; $df = 5$; $P = 0.042$) with higher offspring mortality occurring on larger, rather than smaller, home-ranges (Fig. 3). No relationship was detected between home-range productivity and parameters defining female reproductive performance, including birth rate ($R^2 = 0.011$; $df = 5$; $P = 0.826$), weaning rate ($R^2 = 0.067$; $df = 5$; $P = 0.574$), sexual maturity rate ($R^2 = 0.008$; $df = 5$; $P = 0.852$), or mortality rate ($R^2 = 0.354$; $df = 5$; $P = 0.159$).

Seasonality in weaning, births, and conceptions

Significant seasonality in reproductive events was found ($r = 0.755$; $z = 8.557$; $n = 15$; $P = 0.0009$). Births were concentrated in the first half of October, falling during the later part of the rainy season and the early dry season lasting from June to November. Furthermore, the majority of conceptions were estimated to have occurred during the first half of March, coinciding with the end of the dry season from January to April.

Home-range seasonal productivity vs. female reproductive stages

Births observed between 1993 and 2003 showed no significant relationship with seasonal variation in the relative productivity of home-ranges (T -test, $t = -0.232$, $df = 6$, $P = 0.824$). Similarly, there was no significant relationship between productivity and lactation peak ($t = -0.149$, $df = 6$, $P = 0.887$), but a significant relationship was found between food availability and conception, in which conceptions were clustered during the

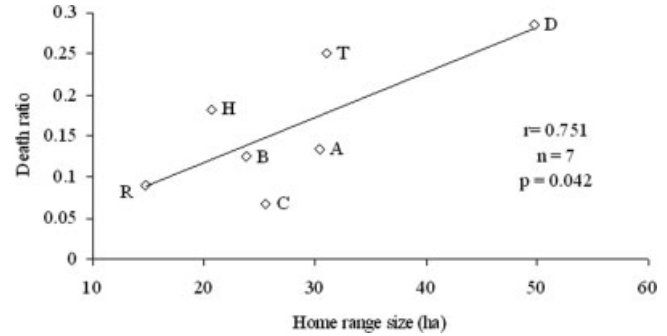


Fig. 3. Offspring mortality ratio vs. home-range size expressed in hectares ($r = 0.751$, $n = 7$, $P = 0.042$).

most productive season ($t = 2.663$, $df = 6$, $P = 0.037$) (Fig. 4).

DISCUSSION

A well-habituated, wild white-handed gibbon population (*Hylobates lar*) has been studied for about two decades at Khao Yai National Park, Thailand, where food productivity was found to vary seasonally. Seasonal variation in food availability was also reflected in reproductive seasonality, as females usually conceived when food was most abundant. However, a trend was only found when comparing home-range quality variation between groups. Female reproductive performances did not differ across females, but significantly more offspring died on larger home-ranges.

Food productivity is considered an important factor influencing female body condition, and hence it may influence reproductive performance for various long-lived animal species (Chastel et al., 1995). In Gombe chimpanzees, for example, nutritional stress resulted in lower female fertility (Wrangham, 1977). In contrast, higher reproductive performance was observed in provisioned compared to un-provisioned Japanese macaques and declined once provisioning ceased (Takahata et al., 1998). In our study, no correlation between female reproductive performance and the quality of home-ranges was detected.

Likewise, in a study of wild capuchin monkeys (*Cebus apella nigritus*), no difference in female reproductive output was detected, despite strong variation in resources available to females because of the provisioning of one group. However, offspring mortality was higher in the non-provisioned group (Di Bitetti and Janson, 2001). Our study did not reveal a relationship between offspring mortality and home-range food productivity, but rather found there to be a positive correlation between offspring mortality rate and home-range size. Elsewhere, we have shown that in our population home-range size and home-range quality are negatively correlated (Savini et al., manuscript). Thus, we assumed that offspring living on larger home-ranges have to travel farther to visit more dispersed resources to satisfy their nutritional needs, and we suggest that an increase in daily travel distance explains observed higher offspring mortality on larger home-ranges. The cohort life curve, which considers the entire growth cycle of offspring from birth to sexual maturity, supports our interpretation because it shows an increased mortality rate after weaning, when

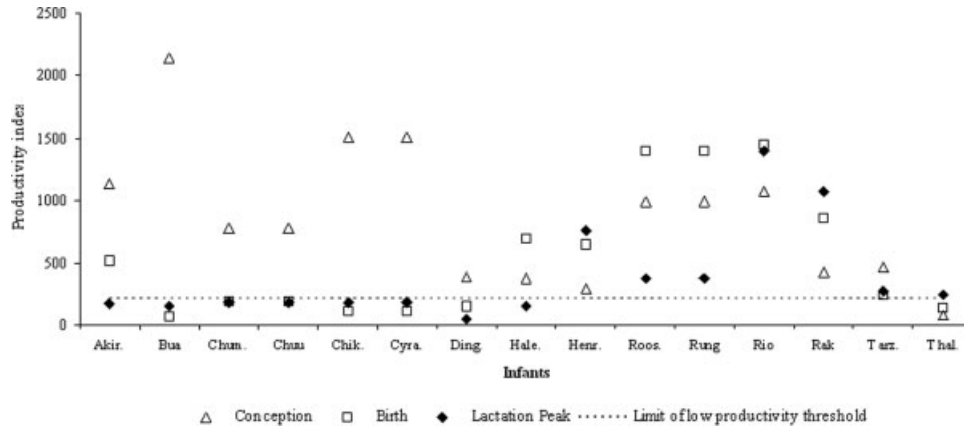


Fig. 4. Productivity index values below the low productivity threshold line indicate a reproductive phase during a period of low food availability.

offspring move independently. Falling during travel has been considered the main cause of death in juveniles because of their relative inexperience with brachiation and jumping, and increased play activities. These factors presumably put juveniles at a higher risk of falling. Falls of juveniles have been noticed in the study site on various occasions (Treesucon, 1984; personal observations), and once a juvenile was temporarily knocked unconscious after a fall (Sommer V., personal communication). Falls are also generally considered the main cause of healed fractures observed in young and adult gibbons (Schultz, 1944). Hence, living on a large home-range may indirectly negatively effect offspring survival as it may lead to longer daily travel distances and an increased probability of a lethal fall. In accordance with this assumption, longer daily travel was observed for group D (1,191 m), the group with the largest home-range, compared to other study groups in which daily travel ranged from 598 to 859 m with an average of 759 ± 118 , (standardized for observation period; $n = 40$; Savini, unpublished data). Overall, daily distance traveled appears to be shorter than what was found for the same species by Raemaekers (1980) in the Krau Game Reserve, Peninsular Malaysia.

The locations of the seven home-ranges we defined by using night-tree to night-tree travel routes were very similar compared to home-range outlines presented by Brockelman et al. (1998) as well as by Raemaekers and Raemaekers (1985) based on their knowledge of locations of the same groups. A lower precision in generating the early home range maps best explains the smaller size and shape variation compared to our data (e.g. note the absence of overlaps). Considering the overall remarkable similarity in study groups' home-range locations, sizes, and shapes at three different points in time, it seemed justifiable to extrapolate that overall home-range locations, sizes, and shapes did not vary significantly over the entire 20 year period. Hence, we assumed that conditions affecting infant travel remained relatively constant over the time we have monitored infant mortality.

Alternatively, the relationship we found between home-range size and increased infant mortality could be interpreted as a chance observation resulting from an exceptionally large-sized home-range, because when

group D is removed from the sample the significant relationship disappeared. We do not think that group D's home-range was exceptionally large, because similar-size ranges have been noticed at other white-handed gibbon sites (Ellefson, 1974; Gittins and Raemakers, 1980). We believe that group D's large home-range was more likely a direct consequence of its location on a south-facing, dry slope of comparatively low resource quality that led to higher offspring mortality. All other home-ranges were located in areas of mixed exposure with overall higher forest quality, resulting in smaller range sizes. We are aware of the somewhat exposed position of group D, but because of the geographic proximity of all of our study groups we considered the inclusion of group D in this analysis very important in allowing us to apply our results to a broad spectrum of possible gibbon habitats.

A second alternative explanation for higher infant mortality on group D's home-range may be related to a higher offspring predation rate because of the larger home-range size. We consider such an explanation unlikely because empirical data of predation events on wild gibbons are lacking (cf. Reichard, 1998; Uhde and Sommer, 2002). Also, group D's home-range was considerably smaller than the size of home-ranges of potential predators (cf. Sunquist and Sunquist, 2002).

It is also possible to hypothesize that the female of group D lost more infants than other females, because she could not provide the same amount of parental care, independent of larger home-range. Perhaps mothering styles vary among gibbon females in our study population, which may expose offspring to different mortality risks. Our sample size was too small to investigate females' mothering behavior and the ways such variation may influence infant survival, but given that the female of group D successfully raised some offspring argues against a consistent difference compared to other gibbon females.

Finally, higher infant mortality observed in group D may have been a stochastic phenomenon that would disappear in a larger sample. Although we are unable to reject this hypothesis, we consider such a scenario unlikely given that we hold the longest time-depth and largest sample size of any wild gibbon study that addresses female reproductive performance, and we see no

qualitative support for such an assumption in our overall population.

Our results on food productivity in the Mo Singto study area clearly indicate the presence of annual seasonal variation, typical of tropical forests (Janson and Chapman, 1999). Two productivity peaks were observed; the first and highest occurred in April with a second and smaller peak in September. The main difference between peaks resides in the number of fruiting species, which was higher during the first peak (with an average of nine species fruiting simultaneously) compared to the second peak (caused largely by fruiting of *Choerospondias axillaris*). We considered the second peak unimportant with regard to female reproduction because fruiting of a single species is unpredictable in time, as circumstances such as unfavorable weather conditions can result in skipping of a fruiting seasons or low production by this species (see Fig. 1). Although a complete failure of fruiting by *C. axillaris* was not observed during our botanical data collection period, changes in the amount of fruits produced and the length of the fruiting period of the species have been noticed across years (UR, personal observation). Additionally, during the first fruiting peak a higher-quality diet can be assumed because of a larger variety of food items. Two low production peaks, or lean periods, were also observed (Fig. 1). As seasonality in reproduction was hypothesized in the Khao Yai population, it is then logical to expect that the seasonality in reproduction observed in the studied population is closely tied to the first fruiting peak.

In the Khao Yai gibbon population births generally occurred during the end of the rainy season when food productivity varied among different groups, and thus no significant relationship was found between the seasonal variation in the quality of each home-range (for birth details see Fig. 4). Similarly, lactation peaks did not appear to be related to food availability in a particular home-range. These results support the interpretation that neither birth nor lactation peak are guiding seasonal reproduction.

Similar to Old World primates, Khao Yai gibbons' conceptions were concentrated during the highest peaks in forest productivity (Fig. 1). A clustering of conceptions coinciding with peak forest productivity have also been reported by Chivers and Raemaekers (1980) on another white handed gibbon population at Kuala Lumpur, Malaysia.

When we investigated in detail the home-range quality available to each female during 15 precisely known conceptions, it was revealed that not all conceptions coincided with periods of higher food productivity but occurred at times when home-range productivity was still on the rise. As observed by Koenig et al. (1997) for Hanuman langurs (*Semnopithecus entellus*), we assume that gibbon females must attain a certain threshold of physical condition necessary to start cycling and to be able to conceive, which can be reached before forest reaches its highest point. In women the capacity to become pregnant is negatively affected by weight loss, as the production of ovarian hormones is directly related to body mass (Green et al., 1988; Lipson and Ellison, 1996). For some females of the Khao Yai population, this threshold appeared to be reached when food availability started to rise and before food productivity peaked, which may represent "over-productivity" in relation to a female's feeding requirements.

Three conceptions occurred during the food resource collection period; two conceptions followed normal infant development, occurring during periods of increasing food production, whereas the third conception occurred after the loss of a suckling infant and during a period of low food availability (December; Thala; Fig. 4). As observed in other primates (Takahashi, 2002), females who suddenly lose an unweaned infant resume cycling sooner than females who wean an infant presumably because body reserves are quickly restored; thus, it may be argued that a female who has lost an infant can conceive sooner (Sommer et al., 1992; Borries, 1997), including during an unfavorable period of the year. A similar effect was observed in seasonally reproducing Phayre's langurs (*Trachypithecus phayrei*) in Phu Khieo Wildlife Sanctuary, Northeast Thailand (Borries C, personal communication).

Overall, our result of seasonal reproduction in gibbons, that is to say the conception peaks during periods of high productivity, highlight the unique taxonomic position of hylobatids within the primate order. Reproductive timing in Khao Yai gibbons was more dependent on ecological factors than what is commonly found for the great apes. Hence, as it was hypothesized, gibbons more closely resemble cercopithecine relatives in reproductive patterns than the other apes. We hypothesize that the similarity in reproduction between gibbons and monkeys is primarily due to a similarity in body size. However, the similarities between the great apes and gibbons in terms of life history traits cannot be overlooked. Gibbon infants develop slower than infants of similarly sized monkeys, gibbon females have gestation and lactation periods of 7 and 22 months, respectively (Treesucon, 1984; Hayssen et al., 1993), and interbirth intervals of approximately 3 years (Hayssen et al., 1993; Reichard, 2003), which puts them closer to patterns found in great apes than similar size monkeys.

Given greater similarity in body size and reproduction between gibbons and monkeys, it would be expected that they evolved a brain size that occurs along the line of body size to brain size ratios found in monkeys. This, however, is not the case because gibbon brains exceed monkey brains by about 45% (Rilling and Insel, 1998). Thus, gibbons combine a small body size of less than 20 kg and reproductive patterns that is similar to monkeys with an enlarged brain size and a life history typical for apes. This suite of gibbon traits questions a co-evolution of body-size and brain-size, which has been argued to have enabled the great apes to evolve complex cognitive capacities including the use of tools for extractive foraging (Begun, 2004; McGrew, 2004; Yamagiwa, 2004; Ward et al., 2004). Extractive foraging has not yet been reported for gibbons, but only future experimental research will show if gibbons may be capable of performing higher cognitive skills despite a small body size, which will contribute to our understanding of the evolution of human cognition.

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