Warren Y. Brockelman · Ulrich Reichard
Uthai Treesucon · Jeremy J. Raemaekers

Dispersal, pair formation and social structure in gibbons (*Hylobates lar*)

Abstract We report observations on reproduction, natal dispersal, pair formation, and group structure based on longitudinal observations of several white-handed gibbon (*Hylobates lar*) groups spanning 18 years. Our observations are at odds with the traditional view that gibbons live in nuclear family groups consisting of a pair of adults and their offspring, and that parents exclude young from the family territory when they reach adult size. In the relatively dense Khao Yai study population, dispersing young usually obtain mates by replacing adults in existing territories, which creates non-nuclear families. Six subadults, five males and one female, matured and dispersed at an average age of 10 years, or about 2 years after reaching adult size. Average natal dispersal distance was 710 m, or between one and two territories away. At least two dispersing males replaced adults in neighboring groups. In one case, forcible displacement of the resident male resulted in a group which included a young juvenile presumably fathered by the previous male, two younger juveniles (probably brothers) from the new male's original group, and (later) offspring of the new pair. Social relations within this heterogeneous group remained harmonious: the adults groomed all the young and play occurred between all preadult members. In only two out of a total of seven cases of dispersal seen did two subadults pair and disperse into new territorial space. Nonreproducing subadults which delay dispersal may be tolerated by the adults provided that they contribute benefits to the adults or their offspring. Possible benefits include behaviors such as grooming, social play with juveniles, and support of the adult male in defending the territory. Delayed dispersal is probably advantageous in a saturated environment where there is no room for floaters, but subadults may also gain indirect fitness benefits by aiding siblings and other relatives.

Key words Gibbon · Pair formation · *Hylobates lar* · Social structure · Natal dispersal

W. Y. Brockelman (✉)
Biology, Faculty of Science, Mahidol University,
Salaya, Buddhamonthon, Nahkon Pathom 73170, Thailand
e-mail: wybrock@st.mahidol.ac.th, Fax: 662-441-1013

W. Y. Brockelman · U. Treesucon
Center for Conservation Biology, Faculty of Science,
Mahidol University, Rama 6 Road, Bangkok 10400, Thailand

U. Reichard
Institut für Anthropologie der Georg-August-Universität,
D-37073 Göttingen, Germany

J. J. Raemaekers
School of Planning and Housing, Edinburgh School of Art,
Lauriston Place, Edinburgh EH3 9DF, UK

Introduction

Dispersal, pair formation (or other arrangements for mating), and social structure are intimately connected. One cannot completely understand pairing or mating behavior without knowing how and when dispersal occurs, and one cannot understand much about social structure and genetic relations without an understanding of both dispersal and mating patterns (Shields 1987; Johnson and Gaines 1990). All of these aspects require long-term studies for their elucidation which have rarely been achieved in long-lived primates (Pusey and Packer 1987).

Our understanding of the social structure of gibbons (Family Hylobatidae) has been based on a simple static model derived from relatively short term studies of only one or two groups. The pioneering work of Carpenter (1940) and Ellefson (1974) on *Hylobates lar* suggested a system of highly territorial, obligately monogamous pairs living in nuclear family groups. Subadult young are forced out of the family group by the same-sexed parent at maturity, to find a mate and a new territory. Most subsequent studies of other gibbon species, including Chivers (1974) on *H. syndactylus*, Tenaza (1975) and Tilson (1981) on *H. klossii*, Gittins (1980) on *H. agilis*, Kappeler (1984) on *H. moloch*, Srikosamatara (1984) on

H. pileatus, and Tilson (1979) on *H. hoolock* appeared to support this simple picture (see reviews by Brockelman and Srikosamatara 1984; Leighton 1987; Dunbar 1988).

Our understanding of natal dispersal and group structure in gibbons has been retarded because we seldom know the ages and birth places of young in groups, or the genetic relationships of individuals in the same and different social groups. In addition, studies have rarely involved more than one habituated group, making it impossible to replicate observations, and virtually precluding the observation of undisturbed intergroup behavior.

The association between monogamy and the participation of both sexes in rearing the brood (Wilson 1975) has tended to predispose us to thinking of monogamous groups as nuclear families. In perennially mated animals in which there is a long period of dependence of young on the adults, however, the genetic structure of the group will depend on the prevailing method of group formation or recruitment of new adults into breeding units. Carpenter (1940) had suggested several possibilities for group formation in northern Thai *H. lar*: (1) pairing of recently matured adults and occupation of a new territory; (2) displacement of one member of a group by an outside usurper; and (3) replacement of one or both members of a pair by maturing offspring on the same territory. Methods (2) and (3) will result in groups which are not nuclear families. Optimal habitat tends to be saturated with gibbon territories (Leighton 1987; Mitani 1990), which should make methods (2) and (3) the most likely methods of group formation or change. In most previous studies of hylobatids (summarized by Leighton 1987), most maturing adults have simply disappeared from the study area unnoticed, but in several reported instances, young have obtained territorial space near or overlapping with their (presumed) parents' territory. In some species that have been relatively well studied (*H. lar*, *H. klossii* and *H. syndactylus*) there are also several instances of mate changes or replacements that would also lead to non-nuclear families (Chivers and Raemaekers 1980; Palombit 1994, Tilson 1981). A displacement of a resident male by a neighboring subadult male in the Khao Yai *H. lar* population has been briefly noted by Raemaekers and Raemaekers (1984a) and Treesucon and Raemaekers (1984); this event will be described in more detail below.

The first person to seriously challenge the nuclear family model in hylobatids was Palombit (1994), who summarized a 6-year history of group changes in *H. lar* and *H. syndactylus* at Ketambe Research Station, Sumatra. Mate desertion and repairing were surprisingly frequent in the six study groups, and gave rise to groups that were not nuclear families. Other processes seen leading to non-nuclear families included father-son replacements, and the dispersal of two or more individuals together. Palombit concluded that "the complexities of social life in these animals extend beyond the narrow limits established by a rigid nuclear family concept".

We present data on lar gibbons in Khao Yai National Park, central Thailand, dating from 1978 and encompassing at least 12 groups, 4 of which are now habituated and 2 others partially so. Our longitudinal 18-year record yields the first data on development rate in the wild, and natal dispersal to pair formation and reproduction (six cases). We discuss the importance of our data with respect to group structure, and benefits of dispersal. We also argue that facultative delayed dispersal is characteristic of gibbons and depends on both intra-group and extra-group factors as suggested in many bird studies (reviews by Koenig et al. 1992; Emlen 1994).

Methods

The Mo Singto study area is located at 730–860 m elevation in seasonally wet evergreen tropical forest in Khao Yai National Park, central Thailand (14 °N). The two adjacent study groups A and F have been observed regularly since January 1978 and group A has been the subject of intensive study of vocalizations (Raemaekers and Raemaekers 1984a,b, 1985a,b) social behavior (Treesucon 1984; Reichard and Sommer 1994; Reichard 1996) and feeding behavior (Whitington and Treesucon 1991). Group A has been habituated to observers since 1981. Six other groups (B, C, E, H, M, and N) also border with A. These have all been observed opportunistically, and groups B and C, the main neighbors of group A, have been studied intensively since 1988 and became habituated in 1992. Groups K and R are new groups which formed during the study. R has been habituated since its adults originated in groups A and B.

The social histories of the gibbon groups at Mo Singto have been pieced together from the observations of 14 different researchers who observed groups during the following periods (numbers of days on which gibbons were observed up to the end of 1995 shown in parentheses):

1. Sompoad Srikosamatara: 1977–1978 (*c*. 40 days)
2. Warren Brockelman: January 1978–December 1995 (126 days scattered throughout period)
3. Jeremy and Patricia Raemaekers: January 1981–October 1982, (*c*. 200 days)
4. Uthai Treesucon: February–May 1981 (*c*. 60 days); January 1982–May 1984 (*c*. 300 days)
5. Duane Quiatt: February–April 1984 (*c*. 60 days)
6. Claudia Whitington: April–June during 1988, 1989 and 1990 (*c*. 75 days)
7. Ulrich Reichard: October 1989–January 1990 (42 days); January 1992–May 1993 (*c*. 250 days); October 1993 (15 days); October 1994 (11 days)
8. Jörg Neudenberger: August–December 1992 (76 days)
9. Anouchka Nettelbeck: February–June 1992 (75 days); June 1995–December 1995 (122 days)
10. Bjarne Klausen: November 1992–February 1993 (*c*. 60 days)
11. Thad Q. Bartlett: October 1993–February 1995 (*c*. 150 days)
12. Nicola Uhde: February–April 1995 (*c*. 45 days)
13. Volker Sommer: September 1994–December 1995 (*c*. 80 days)

Although the observations encompass a total period of at least 18 years, there are gaps in the record during which no observers were at the study site. Gaps of more than 3 months with no observations are as follows: June 1984–December 1986 (18 months); February–June 1987 (5 months); August 1987–February 1988 (7 months); December 1990–April 1991 (5 months); September–December 1991 (4 months); June–September 1993 (4 months). As changes in gibbon groups are relatively infrequent, these gaps do not much affect the long-term record of group histories, but they do affect the precision of timing of certain events such as births, and our knowledge of the changes in social relations among certain individuals.

Gibbons were observed with 8 × or 10 × binoculars. All individuals in groups A, B, C and F could be distinguished by their relative size, pelage color (*H. lar* is asexually dichromatic in central Thailand, with about 52% being brownish black and 48% being light tan or buff; W.Y. Brockelman, unpublished work), and facial features, particularly the shape of the white face ring. Individuals in other groups were known by relative size and coloration only.

An important assumption is that all observers knew and could recognize all individuals in the study groups. This continuity has been maintained mainly by the senior author who has lived in Thailand the whole time and has provided other observers with trail and group territory maps, group lists, previous reports and publications, and general orientations. No one has worked on the gibbons in isolation; it has been standard practice for observers to share notes and general observations. Changes in group structure have usually been verified by all observers working on the site. During the 1990s, the system of gibbon names was unified.

The density of gibbons in this well protected part of the park, about 5 groups km^{-2}, is about the maximum density of *H. lar* seen in Thai forests. As a consequence, there are almost no vacant spaces in which to establish new territories.

Offspring of groups are referred to as A1, A2, F1 and so on, the numbers indicating birth order or order of discovery within the group. Age is generally given in years and months, e.g., 5 y 6 m is 5 years and 6 months. The age classes recognized are infant, small juvenile, large juvenile (or adolescent), subadult (SA) and adult. Our definitions of these classes, based on longitudinal observations in this study, are as follows:

1. 0–2 years, *infant*: carried by mother during travel
2. 2–5 years, *juvenile 1*: independent but small in size; tends to follow mother
3. 5–8 years, *juvenile 2* or *adolescent*: large juvenile but not quite fully grown
4. 8 years–dispersal, *subadult*: full grown but still within territory of parents or "step-parents". Males sing solo near edges of territory.
5. *adult*: mated with territory; sings duets

Results

Synopsis of social changes

Seven subadults, six males and one female, dispersed from groups F, A, B and C, and became members of neighboring groups. An additional adult female replacement was noted in group M. A brief chronology of these events is given below (see also Figs. 1 and 2).

Group F

15 Jan 1978 Group first observed; has 4-year old male juvenile (F1); adult female pregnant.
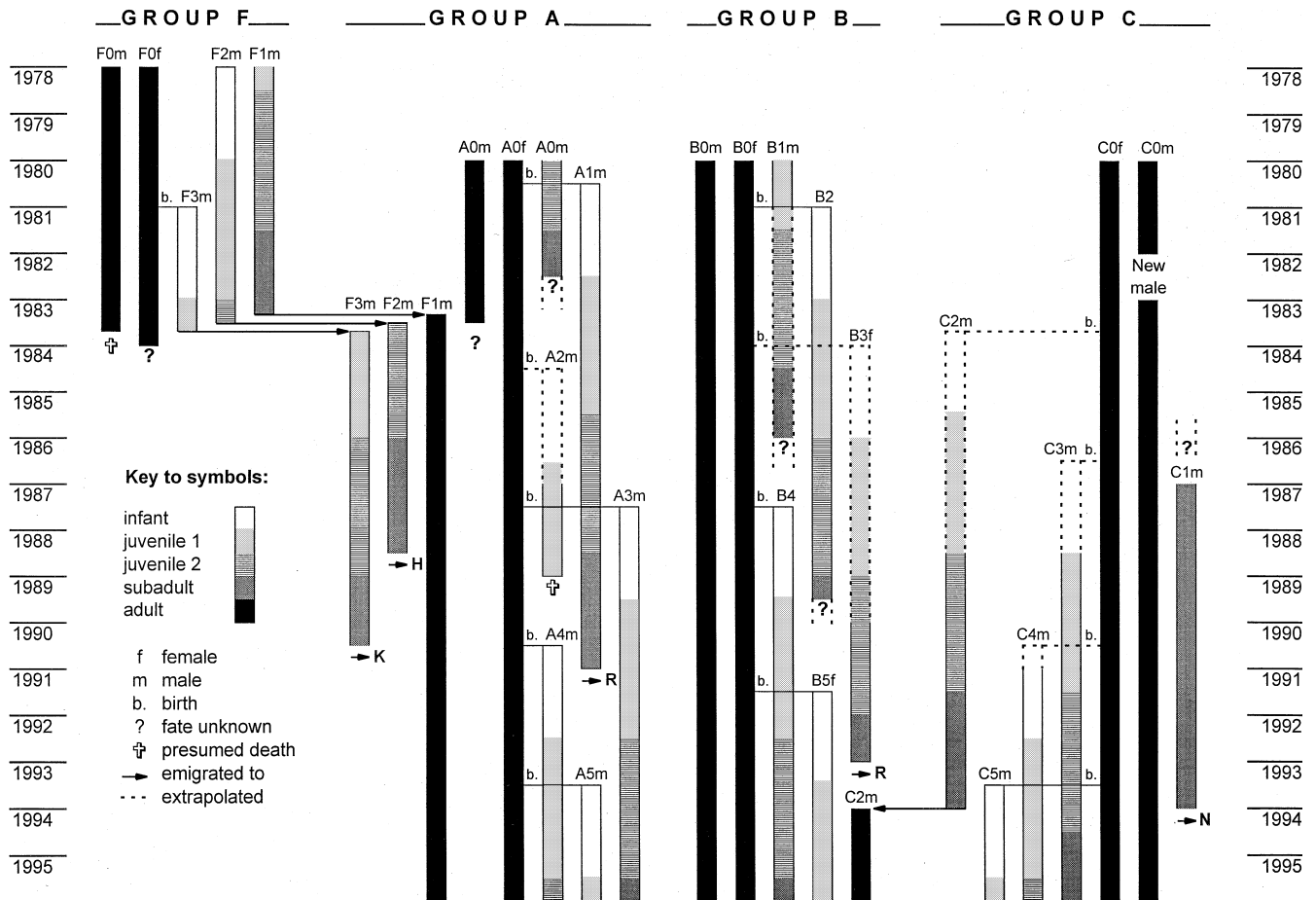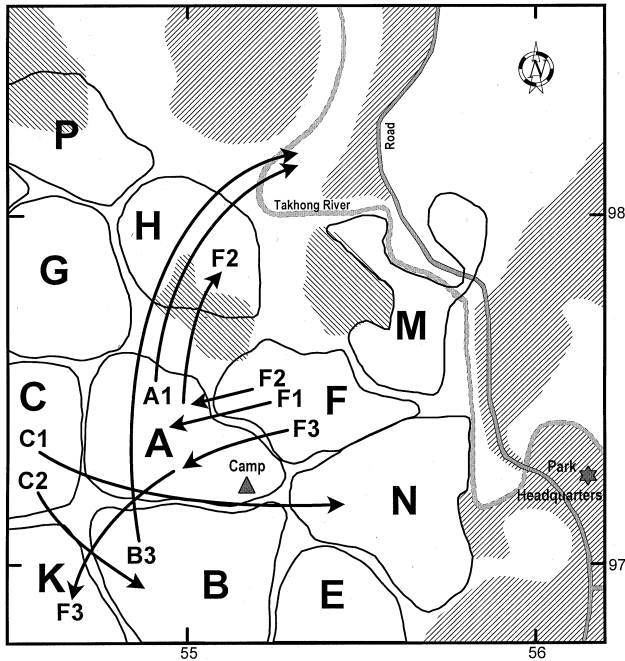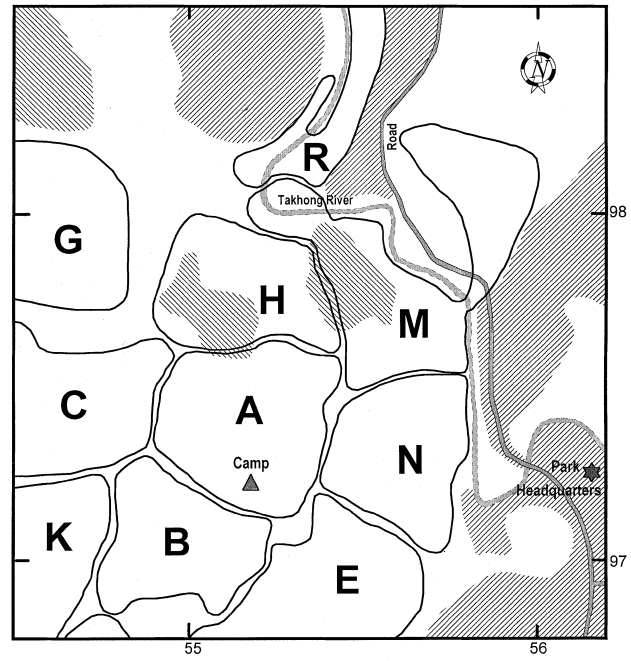

Fig. 1 Changes in composition of groups F, A, B, and C from 1978 to 1995

a

b

17 Jan 1978 Female carrying newborn male infant (F2).

February 1981 Female carrying new male infant (F3). F1 appears to be subadult (SA), about 8 years old. The males F1, F2 and F3 are likely to be full siblings, though due to the possibility of group changes and extra-pair copulations (Reichard 1995), it is possible that they are not. F2 and F3 at least share the same mother.

October 1981 F1 gives solo songs at edge of territory, typical of subadult (SA).

December 1982 Adult male is bitten in territorial conflict (probably with Group A) and wounded in upper arm. Adults no longer duet regularly and adult male has difficulty in keeping up with his group.

January 1983 Adult male disappears; F1 assumes adult male role in territorial defense, and occasionally duets with mother.

June 1983 F1 male leaves territory and within 3 days becomes the mate of the group A female, replacing the group A male (cf. group A below). F1 and the A female duet as a normal mated pair. The actual replacement was not seen, but it is likely that an aggressive displacement occurred.

July 1983 F3 is now juvenile. Adult female leaves territory and moves to new area about 600 m away to the south. F2 and F3 remain and begin to follow neighboring group A, which takes over part of the former group F territory (Fig. 2).

Group A

April 1980 Group consists of adult male and female and adolescent male about 7 years old.

January 1981 Female carries infant about 3 mo old (A1, male). Infant plays frequently with the (now) SA male.

Fig. 2A,B Approximate locations of gibbon group territories in the Mo Singto Study area, Khao Yai National Park. The figures show core defended areas and not the total ranges which overlap considerably. The *vacant areas* above groups P and H were probably utilized by other groups but were not well monitored. *Arrows* show dispersal of subadults from their natal groups, beginning with F1 in 1983. *Shaded areas* are regenerating secondary forest; Grid lines are UTM 1000-m reference lines (1:50,000 sheet 5237 I, Royal Thai Survey Dept.) **A** Before 1990, **B** 1993

26 May 1982 SA male leaves group (fate unknown). Infant play with adult male and female increases greatly, until after weaning.

August 1982 Infant weaned at 22 months of age.

18 June 1983 Adult male displaced by F1 SA; he remains peripheral to the group for several days and then disappears. New adult pair duet very frequently — several times a day.

July 1983 Two juveniles F2, F3 become part of group A.

January 87 New 2.5 years juvenile (male, A2) first seen, presumably first offspring of F1.

July 1987 F2 male, now SA, begins to sing solos in territory. (This behavior, typical of SA males before they leave the parental group, is believed to be a way of advertising to available females in the area.)

1 January 1988 New 3-month infant (A3, male) seen, second offspring after take-over of F1.

6 March 1988 Adult male (F1) acts aggressively toward and chases F2 SA on territorial border.

April 1988 Conflicts with group C encroaching of northwest side of territory increase; also with old rivals group B on southwest side. Males A1 and F3 participate in these. F2 leaves group.

10 December 1988 Juvenile A2 missing; fate unknown.

November 1989 F3 (8 years 11 months) and A1 (9 years

1 months), now both SA, often sing solos in the territory. Adult pair observed to copulate.

June 1990 F3 gone from group. A1 (SA) still present but usually moves about separately.

September 1990 A4 male born.

November 1990 A1 disperses from territory.

16 October 1993 A5 male born.

Dispersals from group A

March 1992 F3 seen with new female 300 m west of territory border (group K); had infant born in late 1990.

11 January 1992 F2 found as adult male of group H 200 m north of territory, with one young juvenile and one adolescent.

16 October 1992 Group H observed to have newborn infant, probably first offspring of F2.

25 March 93 Male A1 found paired with B3 female (new group R) about 800 m north of Group A territory, at forest edge; copulations observed in April.

October 1993 R1 infant born.

Groups B and C

December 1993–March 1994 Group C SA male (C2) sings solos on many mornings near the boundary with group B. Border disputes between B adult male and C males occur almost daily.

February–March 1994 C2 male, now about 10.5 years old, is frequently displaced by the C adult male when the former is grooming or feeding near other group members. The SA learns to retreat at approach of the adult.

10–13 April 1994 C2 SA often away from group C. During April B adult male gives frequent alarm hoots at C2 male.

25 April 1994 C2 male (10 years 6 months old) found soloing in middle of group B territory. The B male tries unsuccessfully to chase him out, usually while giving alarm hoots, over the next 6 months, but C2 just evades the B male's dashes and avoids physical contact. From early 1995 the B male relents and becomes resigned to the presence of the younger male in his territory. Group B contains two juvenile females aged 6 years 5 months and 2 years 6 months.

26 April–23 May 1994 Both males B and C2 duet with the B female, each adding his "coda" to her great-call. After this period, C2 male usually gives the reply and performs most of the duetting in place of the B male.

Group M

25 March 1993 Group M observed to have new adult female (light; previous one, last seen in December 1992, was dark). Resident adolescent and SA male still present; young (3 year 6 months) juvenile seen outside border following another adult or SA (unidentified).

Group N

January 1994 C1 SA male seen in N territory; sings solo during several months afterward. A second new dark male (the previous male was light phase) was seen with group N between October 1994 and June 1995, and then disappeared. C1 pairs with the group N female, apparently without provoking the aggressive chasing and vocalizing that the C2 male did in group B. Fates of other two males unknown.

Behavioral observations of Group A

Of particular interest are the social relations of the members of Group A after the take-over by the SA male of group F. At the time of take-over, Group A had a juvenile offspring (A1) of the previous male about 2 years 8 months old. Within a few months, the juveniles of group F (F2 and F3) became integrated into the new group, which expanded its territory to include most of that of the defunct group F. Their ages at the time of take-over were approximately 5 years 6 months and 2 years 5 months, respectively. Both juveniles initially kept their distance from the adult female, but were groomed frequently by male F1. Over the next few months, however, the female gradually accepted the younger juvenile F3 as a family member, but the older (F2) juvenile never became fully integrated into the group. F3 took part in the daily grooming and play activities which usually occupied about 1 h of the group's resting time during the middle of the day. The adult female was not known to be related to these young, although this cannot be ruled out. The adult male continued to groom his putative younger brothers, and showed no hostility toward them until after they became subadult and began singing solos in the territory.

In 1989 after F2 had disppeared from the territory, the adult male spent about equal amounts of time grooming his presumed younger sibling F3 (26% of grooming time) and the similar-aged A1 male (23%). The adult female in 1989 also groomed F3 even more than her own son (18% vs. 6% of active grooming time). The behavior of the F1 male toward his younger siblings and his step-son was indistinguishable from that expected of a father.

Play was one activity that conspicuously involved all young, including infants, juveniles and some subadults. While A1 was a large infant, 16–24 months old, in 1982, play with its two parents occupied an average of about 45 min of its active time per day (Treesucon 1984). Play was particularly vigorous after A2 became juvenile in 1987, and involved primarily the A1, A2, and F3 males. Play bouts involved wild chases through the branches, pulling of arms and legs, grappling and mock biting. The disappearance of A2, the first offspring born after the new male took over, at approximately age 4 years 5 months, is unexplained; no gibbon was seen to behave aggressively toward him. In 1992, focal animal obser-

vations revealed that juveniles A3 and C3, then 4–5 years old, engaged in social play with their respective group members for an average of more than 1 h per day (Nettelbeck 1993).

Life history information

Maturation

Our sample of young which were followed through dispersal to new pair formation include five males and one female (Table 1). The birth dates of these young were known with varying accuracy; estimated confidence limits are given in the table. The birth dates of F2 and A1 are known to within 1 month, and three others to within an estimated 6 months. These young reached full adult size at approximately 8 years.

Table 1 also gives the approximate ages at dispersal (leaving the parental group) and dispersal distance. All these individuals have formed new pairs and at least four (three males and one female) have produced new offspring, assuming, of course, that they were not cuckolded. Extra-pair copulations (EPCs) have been seen in this population by Reichard (1995), and U. Suwanvecho (personal communication). Reichard (1995) estimated that they make up about 12% of all copulations. The possibility of EPCs may render the estimated age at first reproduction (birth of first offspring) for males a slight underestimate. The infant seen in group K, to which F3 dispersed, is excluded because it was possibly fathered by the previous mate of the K female before F3 arrived. The age of dispersal averaged 10 years for the males and was about 8.6 years for the B3 female. The age at birth of first offspring averages 12.9 years for the three males and was 9.75 years for female B3. At the time of writing the C2 male had not produced an offspring by the age of 14 years.

Natal dispersal distance

The mean natal dispersal distance of six maturing individuals was 710 m (range 300–1400 m; Fig. 2). For the five males, average dispersal distance was 620 m. Since the average territory is around 400–500 m in diameter in Khao Yai, these gibbons thus dispersed to areas only one or two territories away. Three of the gibbons dispersed into a territory bordering their natal group. One additional subadult male (C1) of unknown age in group C dispersed a distance of about 1000 m to group N (Fig. 2a) (there is insufficient evidence that he was born in group C). There is no evidence that dispersal distance differs between males and females.

It is of interest to know to what extent these dispersing individuals might represent a biased sample, which could occur if unrelocated animals had tended to disperse farther than those that were relocated (Koenig et al. 1996). During the time of the study, there were no gibbons in habituated groups which disappeared upon dispersal and could not be subsequently located. There were, however, several gibbons from unhabituated groups which dispersed without being located. This includes two older siblings of B3 which left before group B became habituated in 1992, and three individuals of group M, which was never habituated or observed regularly, and one or two young in group H. One maturing female in unhabituated group N also disappeared some time in 1995. Maturing young from unhabituated groups could not easily be relocated because their pelage and facial features were not well enough known and they could not be seen well enough to permit positive identification after dispersal. Thus, we cannot deny the possibility that some animals disperse much farther than 1 km, but our observations suggest that they are in the minority.

Pair formation

At least four of the dispersing males (F1, F3, A1, C1) formed a new group through replacement of a male in an existing group, but only in the case of F1 was the resident male known to have been forcibly displaced. Groups H and K were not observed immediately prior to the arrival of the new male. Forcible displacement of the N male by C1 was likely, but group N was not being observed regularly during that time. The continued

Table 1 Age and distance of natal dispersal of subadult gibbons from groups in the Mo Singto study area, Khao Yai Park

Individual code[a]	Date of birth (month/year, ±)[b]	Age at dispersal (year-month)	Age at first offspring (year/month)	Dispersal distance (m)[c]
B3fD	1/84, 5 m	8–7	9–9	1,400
F1mL	7/73, 6 m	9–11	11–0	300
F2mL	1/78, 1 day	10–2	14–9	400
F3mL	1/81, 5 m	9–4	10–4?[d]	900
A1mL	10/80, 1 m	9–11	13–0	1,000
C2mL	10/83, 1 y	10–6	?[e]	500

[a] Code indicates group of origin, birth order, sex, and pelage color phase (L = light, D = dark)
[b] ± represents estimated confidence interval of birth date, based on estimated age when first seen
[c] Measured from approximate centers of territories
[d] Paternity of infant seen in F3's new group uncertain
[e] C2 male has not yet fathered an infant

presence of young aged about 3 and 6 years in Group H after the arrival of the new male implies that the only change was the replacement of the old male by the new one, F2. Group K may have been altered by a male take-over, as the infant seen when male F3 was rediscovered in Group K was estimated to be about 1 year 6 months old, and could have been fathered by a previous male. The K female looked relatively old, with pendulous nipples. Group R (with male A1 and female B3) was formed without any take-over.

The composition of Group M, previously an all-dark phase group, was altered in early 1993 through a take-over by a light phase adult female of unknown origin. Judging from her pendulous nipples, this female was previously parous. Just after the take-over, the group included two SA males, a 6-year-old adolescent and a young juvenile of 2 years 6 months. Two months later one of the SA males and the young juvenile were seen just outside the territory, the juvenile following another dark adult-size individual that may have been its mother.

Territorial boundary changes

Male F1 took over group A in June 1983, and by July his presumed brothers (F2 and F3) had also joined group A (Fig. 1), after the presumed death of the adult male and the subsequent abandonment of the territory by the adult female. With both adults gone, Group F was now dissolved. Group A then usurped about half the territory of group F. In late 1987, after the birth of A3, Group A contained seven members, the largest number ever seen in a group in Khao Yai. The territory had increased from about 18 ha before the take-over to 26 ha. The now fully grown F2 male was chased by the adult male on the border near the old territory of group F; F2 left the home range of group A in 1988. Conflicts between groups A and C on the northwest side of A's territory increased, and in 1989, the two new SA (A1 and F3) participated in these, helping to maintain the territorial boundary. Group C had one SA, or one extra non-breeding adult, male in 1988, but by 1990 the older adolescent was maturing into another SA. Thus in 1991, when group A had lost its two SA, group C had attained greater strength with two extra adult-size males aged about 8 and 12 years. All three males helped defend group C's boundary against A through 1993, and group C expanded its territory about 150 m into group A's, which was reduced to about 20 ha. The group A male could not easily maintain his territorial boundary against the group C males, and border clashes were numerous.

Discussion

Dispersal and pair formation

The average age at dispersal of the five young males followed in our study was around 10 years, which indicates that they spent an average of 2 years on the parental territory after reaching physical maturity. The age at which the Khao Yai gibbons reach adult size, approximately 8 years, is older than commonly assumed for wild gibbon populations (Leighton 1987) and is considerably older than that reported for many gibbons in zoos (e.g., Geissmann 1991) Our observations indicate that delayed dispersal was the rule in this population and that considerable tolerance was shown by the resident breeding adults toward young individuals of potential breeding age.

The population in Khao Yai appears to be at maximum density, and there is little vacant forest area which is not being defended by existing groups. This limits the dispersal opportunities of subadults. The situation has much in common with that reported for communally breeding birds, in which the decision of whether to remain a helper in the parental group or risk the hazards of dispersal is influenced by the availability of new territorial space and available mates (Brown 1974; Emlen 1982, 1991; Gaston 1978; Woolfenden and Fitzpatrick 1978, 1984), as well as by the opportunities for increasing ones fitness indirectly by helping at the parents' nest (Stacey and Ligon 1987; Koenig et al. 1992). The options available to dispersing gibbons in a saturated environment are precisely the same as those described by Emlen (1982) for communally breeding birds: (1) challenge and defeat a territory holder; (2) compete for and fill the vacancy left by the death of a territory holder; and (3) inherit or bud off a portion of the parental territory. Male F1 managed a combination of methods 1 and 3. Male F2 succeeded in finding a territory and mate by either method 1 or 2. The C1 male and the new female in group M most likely challenged and defeated the like-sexed adult. Option (1) also seems likely in the case of male F3.

A new and unexpected option seems to have been invented by male C2 who, impervious to the aggression of the male of group B, took up residence in his territory and became a member of the group. Only one new pair, subadults male A1 and female B3, managed to find some new territorial space at the edge of the forest. This option probably does not present itself often in this part of Khao Yai Park.

Replacing an adult on an existing territory is probably the most feasible option in this population because new potential mates do not become available frequently. With a birth rate averaging no more than one young per female per 3 years and survivorship to maturity of approximately 50% (based on analysis of a stationary age distribution; W.Y. Brockelman, unpublished work), a given neighboring territory will produce a potential new mate of the right sex on average once per 12 years. Chance fluctuations in the sex ratio will exacerbate the problem. Obtaining a mate through replacement also has the advantage of allowing the subadult to move onto a full-sized territory with a resident that already knows well the locations of food sources. This method of acquiring a mate, however, has not been found to be

common in other studies. In the cases of mate change observed by Palombit (1994) in Ketambe, Sumatra, in *H. lar* and *H. syndactylus*, death or apparent desertion by one of the pair was the precipitating factor. In the other major long-term study of the same species at Kuala Lompat, Malaysia (Raemaekers and Chivers 1980), mate displacement was responsible for only 1 out of 11 pairbond terminations (summarized by Palombit 1994). Mate desertion has not been noted in the Khao Yai study area, but whether replacement in the cases of F2 and F3 was forcible or not is not known.

Although replacement of an adult residing on a territory would seem to be a risky option, in reality it may not always be. A dispersing subadult would presumably not attempt a forcible displacement unless he or she were confident of succeeding. Frequent encounters with neighbors must allow subadults to monitor the strength of like-sexed territory holders, as well as the suitability of their mates. Moreover, a subadult apparently does not disperse until he or she has located a potential mate in a nearby territory. This is consistent with the rarity of nonterritorial adult-sized animals, or floaters, seen in gibbon study areas (Leighton 1987). A high mortality rate among floaters might also explain their rarity (Mitani 1990), but our findings suggest that if the mortality of floaters is high, delaying dispersal is a way of avoiding it.

Our observations thus provide an example in which dispersal is advantageous in a stable saturated environment (Hamilton and May 1977; review in Johnson and Gaines 1990). Dispersal is facilitated in gibbons because there is apparently no cost to dispersal *per se* provided that the distance is short.

The short average natal dispersal distance of about 700 m is consistent with the relatively few data from other studies, particularly those of Tilson (1981) for *H. klossii*, in which dispersing young nearly always (seven out of eight cases) established themselves on or adjacent to the presumed parental territory. However, that study and most others were too short to be able to ascertain both the natal territory and subsequent breeding.

The short dispersal distance in gibbons indicates a genetically viscous population with a moderate level of inbreeding (Shields 1982, 1987; Chepko-Sade et al. 1987). As siblings and cousins will commonly exist in neighboring territories, it seems inescapable that matings between relatives will be common. It is important to know, however, whether gibbons avoid close inbreeding (mating with parents, offspring or full siblings) by dispersing out of the natal territory.

The many possible reasons for dispersal can be reduced to three major categories (Greenwood 1980; Dobson 1982; Waser and Jones 1983; Johnson and Gaines 1990). These are: (1) avoidance of inbreeding; (2) obtaining a mate; and (3) obtaining resources. Avoidance of inbreeding as the primary reason for dispersal is somewhat controversial (e.g., Moore and Ali 1984; Dobson and Jones 1985; Shields 1982, 1987); hence we tend to favor other more obvious benefits unless they

can be excluded. Our limited data suggest that all three reasons for dispersal probably operate in gibbons, though not necessarily all at the same time. In the case of the dispersing A1 male and B3 female, acquisition of territorial space was a sufficient reason for travelling farther than 1 km. In the cases of males F2, F3, C1 and C2, acquisition of a mate and a territory were both probable (and inseparable) reasons for dispersal. The case of F1, however, critically supports the inbreeding avoidance hypothesis, because before dispersal, the young male had both a territory and a potential mate (his mother), with whom he duetted after the disappearance of his (presumed) father. The subadult F1 still dispersed, leaving close inbreeding avoidance as the only obvious explanation. Thus, our observations suggest that the causes of dispersal are not mutually exclusive (Dobson and Jones 1985), and they may vary from one individual to another. In gibbons, the small group size and the small number of mating possibilities in the immediate neighborhood cause each individual to be faced with a unique situation and a somewhat different set of incentives for dispersal.

Group structure

A few instances of new group formation have been witnessed in gibbons, involving the pairing of subadults or other apparently unmated individuals, usually in space adjacent to the parental territory (*H. syndactylus*: Gittins and Raemaekers 1980; *H. lar*: Chivers and Raemaekers 1980; MacKinnon and MacKinnon 1977; Palombit 1994; *H. pileatus*: Srikosamatara 1984; *H. klossii*: Tilson 1981). Group change through replacement of adults on existing territories (e.g. Chivers and Raemaekers 1980 for *H. syndactylus*) often may have escaped observation because it occurs rapidly and leaves no lasting evidence if the observer is not familiar with the individual animals in surrounding groups. There have, however, been more numerous reports of adult gibbons remating after the loss of a mate due to death, disappearance or apparent desertion (reviewed by Palombit 1994). Although groups modified through either displacements or replacements of adults will not be true nuclear families, they may resemble nuclear family groups in age-sex composition and general social behavior. The only obvious clue that a group is not a nuclear family may be the presence of young less than 2 years apart in age. We now know that offspring from one female are not likely to be as close as 2 years apart, as mothers nurse their infants for about 2 years, and copulations between adults resume within about 18 months after parturition and reach a peak at the time of weaning (Treesucon 1984). Our long term observations in Khao Yai indicate a minimum birth interval of about 3 years.

In a census of 64 *H. lar* groups in Khao Yai Park (W. Y. Brockelman, unpublished work), 33% of groups contained young estimated to be 2 years or less apart.

Although subjective aging of individuals in the forest by size is prone to some error, the data suggest that the existence of groups with young from more than one family must be a regularly occurring phenomenon. Our group A existed as a non-nuclear family for 7 years, and during our study at least 4 other groups (B, H, M, N, and perhaps K) became similarly modified. This represents the majority of groups that have been observed intensively.

Demographic considerations lend more support to our suspicion that many, if not most, groups are not nuclear families, and possibly contain half-siblings, nieces, nephews and even unrelated individuals from changes in pair-bonds. The annual adult survival rate of adults has been estimated (based on the ratio of non-adult gibbons to adults in the population and estimates of recruitment; W.Y. Brockelman, unpublished work) to be as high as 94% per year. At this rate, the chance that an adult will survive 8 years until a given offspring reaches subadulthood is $0.94^8 = 0.61$. The chance that a given young will lose at least one of its parents before becoming a subadult is then $1-0.61^2 = 0.628$ or about 63%. Many young in groups reconstituted from broken families must undoubtedly thrive, but no single-adult family units seem to exist for long in gibbons. Although the use of duets as an auditory aid in locating groups could bias our sample against broken family units, we believe that such units would have been found in greater numbers during our field research if they were not very unstable and transitory.

Social behavior in nonfamily groups

The observed pair-bond changes in gibbons and resulting changes in family group structure show that gibbons can adapt behaviorally to a variety of group living arrangements. This raises important new questions about the behavioral relations between the adults, who should have control over group composition, and other members who may not be close relatives, and young who stay beyond their tenure as dependents.

In primates such as marmosets and tamarins that are frequently, though not exclusively, monogamous, kin other than direct offspring may aid in rearing young (Dawson 1977; Neyman 1977; Kleiman 1981; Rylands 1981; Soini 1982; Terborgh and Goldizen 1985; Goldizen 1987a,b; Sussman and Garber 1987). This has apparently not been reported in the monogamous cebids, although extra nonbreeding adults have been reported in some groups of *Aotus* and *Callicebus moloch* (Robinson et al. 1987). For parents to tolerate individuals other than direct offspring in the group, there should be reciprocal benefits (Kleiman 1981). The argument must also apply to offspring that are permitted to remain in the group as subadults. We believe that such benefits exist in the case of non-nuclear family members in gibbons, although they do not include help given in carrying or feeding young offspring. In general, the major benefits accruing to the adult pair and their offspring probably include (1) improved physical and social development of large infants and juveniles through play and grooming; and (2) aid in territorial defense. With a birth interval of 3–4 years, it is common for juveniles to have few or no nonadult playmates; 16 out of 64 lar groups censussed, when first seen, had a single infant or juvenile as the only non-adult.

Acrobatic social play should improve locomotory ability and coordination and may help to develop social relationships (Baldwin and Baldwin 1977; Fagen 1980), but the extent to which social play improves the fitness of individuals later in life is still largely untested (Martin and Caro 1985; Caro 1988). Fagen has remarked on the relatively small amount of play behavior reported for wild gibbons, primarily from the study of Ellefson (1974) on *H. lar* which reported about 10 min of play per day for a juvenile. Ellefson (1974) nevertheless described both solo and social play in considerable detail. Social play in gibbons is usually very acrobatic, involving rapid brachiation and chasing, diving through the air, grasping limbs, wrestling and mock biting. Gittins and Raemaekers (1980) recorded 1 min or less of play per day for *H. lar* and *H. agilis*, but this was an average for all group members. Whitten (1984) reported no play in the activity budget of *H. klossii*, but mentioned play between the mother and female juvenile in a narrated story of his study group (Whitten 1982). It is likely that the interval and scan sampling methods for activity budgets used by most previous observers have tended to underestimate the time spent in play.

Our Khao Yai study groups have been found to engage in considerably more social play than reported in previous studies (Treesucon 1984; Reichard 1991; Nettelbeck 1993). Play has been found to occupy 1 h or more per day for juveniles, and play bouts involving two or three individuals often lasted for 0.5 h or more. Social play begins in the first year of life of the infant. During the first year of infancy of the A1 male, he played mostly with the group A subadult. When the subadult left the group, the parents became the infant's play partners (Treesucon 1984).

The other major benefit of having extra members in the group is in defence of the territory (see Chivers and Raemaekers 1980 for an example). The presence of subadult males that help the adult male defend the territory makes it more difficult for neighboring groups to claim extra territory and probably reduces the chance that the resident adult male will be displaced. Such benefits, however, would be at least partly offset by the extra demand the subadults place on the territory's food resources.

An additional benefit to the adult male in having subadults in the territory is that it creates opportunities for extra-pair copulations with neighboring adult females. In early 1993, Reichard (1995) observed several such copulations involving the adult female of group A. In one instance, the group A male was involved in an encounter with a subadult of group C when the adult

male of C rushed into the territory of group A and achieved a copulation with the female.

In conclusion, the lessons from our study are several: that gibbon group structure is more variable and less easily characterized than previously thought; that gibbon social development and mating opportunities are highly variable individually; and that intragroup behavior cannot be understood separately from a thorough study of intergroup interactions and changes. Further advances in our understanding of gibbon social behavior will also depend on finding ways of ascertaining relationships more accurately using molecular genetic techniques.

References

Baldwin JD, Baldwin JI (1977) The role of learning phenomena in the ontogeny of exploration and play. In: Chevalier-Skolnikoff S, Poirer FE (eds) Primate bio-social development: biological, social, and ecological determinants. Garland, New York, pp 343–406

Brockelman WY, Srikosamatara S (1984) Maintenance and evolution of social structure in gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds) The lesser apes: evolutionary and behavioural biology. Edinburgh University Press, Edinburgh, pp 298–323

Brown JL (1974) Alternative routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am Zool 14:63–80

Caro TM (1988) Adaptive significance of play: are we geting closer? Trends Ecol Evol 3:50–54

Carpenter CR (1940) A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). Comp Psychol Monogr 16(5):1–212

Chepko-Sade BD, Shields WM, Berger J, Halpin ZT, Jones WT, Rogers LL, Rood JP, Smith AT (1987) The effects of dispersal and social structure on effective population size. In: Chepko-Sade BD, Halpin ZT (eds) Mammalian dispersal patterns. University of Chicago Press, Chicago, pp 287–321

Chivers DJ (1974) The siamang in Malaya: a field study of a primate in tropical rain forest (Contributions in Primatology, vol 4). Karger, Basel

Chivers DJ, Raemaekers JJ (1980) Long term changes in behavior. In: Chivers DJ (ed) Malayan forest primates: ten years' study in tropical rain forest. Plenum, New York, pp 209–258

Dawson GA (1977) Composition and stability of social groups of the tamarin, *Saguinus oedipus geoffroyi,* in Panama: ecological and behavioural implications. In: Kleiman DG (ed) The biology and conservation of the Callitrichidae. Smithsonian Institution Press, Washington, pp 23–37

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Dobson FS, Jones WT (1985) Multiple causes of dispersal. Am Nat 126:855–858

Dunbar RIM (1988) Primate social systems. Croom Helm, London

Ellefson JO (1974) A natural history of white-handed gibbons in the Malayan Peninsula. In: Rumbaugh DM (ed) Gibbon and siamang, vol 3. Karger, Basel, pp 1–136

Emlen ST (1982) The evolution of helping. I. An ecological constraints model. Am Nat 119:29–39

Emlen ST (1991) Cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology, an evolutionary approach, 3rd edn. Blackwell, Oxford, pp 301–335

Emlen ST (1994) Benefits, constraints and the evolution of the family. Trends Ecol Evol 9:282–285

Fagen RM (1980) Animal play behavior. Oxford University Press, Oxford

Gaston AJ (1978) The evolution of group territorial behavior and cooperative breeding. Am Nat 112:1091–1100

Geissmann T (1991) Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.) Am J Primatol 23:11–22

Gittins SP (1980) Territorial behavior in the agile gibbon. Int J Primatol 1:381–389

Gittins SP, Raemaekers JJ (1980) Siamang, lar and agile gibbons. In: Chivers DJ (ed) Malayan forest primates: ten years' study in tropical rain forest. Plenum, New York, pp 63–105

Goldizen AW (1987a) Tamarins and marmosets: communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 34–43

Goldizen AW (1987b) Facultative polyandry and the role of infant-carrying in wild saddle-backed tamarins (*Saguinus fuscicollis*). Behav Ecol Sociobiol 20:99–109

Goldizen AW, Terborgh J (1986) Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). In: Else J, Lee P (eds) Primate ecology and conservation. Cambridge University Press, Cambridge, pp 191–198

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hamilton WD, May RM (1977) Dispersal in stable habitats. Nature 269:578–581

Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu Rev Ecol Syst 21:449–480

Kappeler M (1984) Vocal bouts and territorial maintenance in the moloch gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds) The lesser apes: evolutionary and behavioural biology. Edinburgh University Press, Edinburgh, pp 376–389

Kleiman DG (1981) Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior: recent research and new theory. Chiron, New York, pp 332–344

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150

Koenig WD, Vuren D van, Hooge, PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517

Leighton DR (1987) Gibbons: territoriality and monogamy. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 135–145

MacKinnon J, MacKinnon K (1977) The formation of a new gibbon group. Primates 18:701–708

Martin P, Caro TM (1985) On the functions of play and its role in behavioral development. In: Rosenblatt JS, Beer C, Busnel M-C, Slater PJB (eds) Advances in the study of behavior, vol 15. Academic Press, Orlando, pp 59–103

Mitani JC (1990) Demography of agile gibbons (*Hylobates agilis*) Int J Primatol 11:411–424

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Nettelbeck AR (1993) Zur Öko-Ethologie freilebender Weiss-handgibbons (*Hylobates lar*) in Thailand. Diplomarbeit, University of Hamburg, Hamburg

Neyman PF (1977) Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Kleiman DG (ed) The biology and conservation of the Callitrichidae. Smithsonian Institution Press, Washington, pp 39–71

Palombit R (1994) Dynamic pair bonds in hylobatids: inplications regarding monogamous social systems. Behaviour 128:65–101

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 250–266

Raemaekers JJ, Chivers DJ (1980) Socio-ecology of Malayan forest primates. In: Chivers DJ (ed) Malayan forest primates: ten years' study in tropical rain forest. Plenum, New York, pp 279–316

Raemaekers JJ, Raemaekers PM (1984a) Loud calls of the gibbon (*Hylobates lar*): repertoire, organization and context. Behaviour 91:146–189

Raemaekers JJ, Raemaekers PM (1984b) Vocal interactions between two male gibbons, *Hylobates lar*. Nat Hist Bull Siam Soc 32:95–106

Raemaekers JJ, Raemaekers PM (1985a) Long-range vocal interactions between groups of gibbons (*Hylobates lar*). Behaviour 95:26–44

Raemaekers JJ, Raemaekers PM (1985b) Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. Anim Behav 53:481–493

Reichard U (1991) Zum Sozialverhalten einer Gruppe freilebender Weisshandgibbons (*Hylobates lar*). Diplomarbeit, University of Goettingen

Reichard U (1995) Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). Ethology 100:99–112

Reichard U (1996) Sozial- und Fortpflanzungsverhalten von Weisshandgibbons (*Hylobates lar*); eine Freilandstudie im Thailaendischen Khao Yai Regenwald. PhD. dissertation, University of Goettingen

Reichard U, Sommer V (1994) Grooming site preferences in wild white-handed gibbons (*Hylobates lar*). Primates 35:369–374

Robinson JG, Wright PC, Kinzey WG (1987) Monogamous cebids and their relatives: intergroup call and spacing. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 44–53

Rylands AB (1981) Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuana, Mato Grosso. Primates 22:46–59

Shields WM (1982) Philopatry, inbreeding, and the evolution of sex. State University of New York, Albany

Shields WM (1987) Dispersal and mating systems: investigating their causal connections. In: Chepko-Sade BD, Halpin ZT (eds) Mammalian dispersal patterns. University of Chicago Press, Chicago, pp 3–24

Soini P (1982) Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. Fol Primatol 39:1–21

Srikosamatara S (1984) Ecology of the pileated gibbon (*Hylobates pileatus*) in Southeast Thailand. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds) The lesser apes: evolutionary and behavioural biology. Edinburgh University Press, Edinburgh, pp 242–257

Stacey PB, Ligon JD (1987) Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. Am Nat 130:654–676

Sussman RW, Garber PA (1987) A new interpretation of the social organization and mating system of the Callitrichidae. Int J Primatol 8:73–92

Tenaza RR (1975) Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. Foll Primatol 24:60–80

Terborgh J, Goldizen AW (1985) On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). Behav Ecol Sociobiol 16:293–299

Tilson RL (1979) Behavior of hoolock gibbon (*Hylobates hoolock*) during different seasons in Assam, India. J Bombay Nat Hist Soc 76:1–16

Tilson RL (1981) Family formation strategies of Kloss's gibbons. Foll Primatol 32:259–287

Treesucon U (1984) Social development of young gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. MSc dissertation, Mahidol University, Bangkok

Treesucon U, Raemaekers JJ (1984) Group formation in gibbon through displacement of an adult. Int J Primatol 5:387

Waser PM, Jones WT (1983) Natal philopatry among solitary mammals. Q Rev Biol 58:355–390

Whitten AJ (1982) The gibbons of Siberut. Dent, London.

Whitten AJ (1984) Ecological comparisons between Kloss gibbons and other small gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds) The lesser apes: evolutionary and behavioural biology. Edinburgh University Press, Edinburgh, pp 219–227

Whitington C, Treesucon U (1991) Selection and treatment of food plants by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. Nat Hist Bull Siam Soc 39:111–122

Wilson EO (1975) Sociobiology. Harvard University Press, Cambridge

Woolfenden GE, Fitzpatrick JW (1978) The inheritance of territory in group-breeding birds. Bioscience 28:104–108

Woolfenden G, Fitzpatrick J (1984) The Florida scrub jay: demography of a cooperative breeding bird. Princeton University Press, Princeton

Communicated by A.E. Pusey