Varying Ecological Quality Influences the Probability of Polyandry in White-handed Gibbons (*Hylobates lar*) in Thailand

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ABSTRACT

Although members of the family Hylobatidae are known to be monogamous, adult white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand, also show multimale groups and polyandry. A need for more than one male to successfully raise offspring cannot explain the occurrence of polyandry in these territorial primates, because direct paternal care is absent in this species. We hypothesize that polyandry is primarily related to costs/benefits for males of cooperatively defending a female and/or resources; our prediction was that polyandry would become more frequent with increasing costs of female/resource defense. We measured the ecological quality of seven gibbon home ranges over a 3-yr period (2001–2003) to investigate how resource availability affected the probability of polyandry, and found a significant negative relationship between home range quality and home range size. Larger home ranges were of lower quality. As predicted, groups living on larger, poorer home ranges also experienced longer periods of polyandry. In forest areas of comparatively low quality, acquiring and maintaining a large home range that includes enough resources for a female to reproduce steadily may surpass a single male's capacity. Our model of cooperative male polyandry was supported by preliminary data of shared territorial defense and access to the female. However, interaction proportions were strongly skewed, and female's primary male partners monopolized grooming and mating. Nevertheless, a primary male on a large territory may benefit from the presence of a secondary male with aid in territorial/female defense, whereas a secondary male may gain by avoiding high dispersal costs.

Key words: home range quality; Khao Yai National Park; monogamy; multimale groups; Thailand.

IT IS BROADLY ACCEPTED IN BEHAVIORAL ECOLOGY that the distribution of mammalian females is primarily determined by the distribution of environmental risks and resources whereas males tend to map themselves onto the spatial and temporal distribution of receptive females (Wrangham 1980, van Schaik 1983, Sterck *et al*. 1997, Kappeler & van Schaik 2002). Since male and female reproductive strategies do not always coincide, observable social organizations and mating systems are best understood as the emerging, visible compromises between males' and females' reproductive interests (Davies 1992). Among these compromises, polyandry, when two or more males live and mate with one female, is a rare outcome in birds and mammals (Arnold & Owens 1998, Ligon 1999).

The advantages for females from polyandrous mating are straightforward (Hrdy 2000). They can benefit indirectly by increasing their conception probability—especially if faced with a risk of temporary or permanent male sterility (Gromko *et al*. 1984) —by producing genetically superior offspring as a result of sperm competition (Põldmaa & Holder 1997, Yasui 1997), by reducing the risk of infanticide, by confusing paternity (Hrdy 1979). Or they can benefit directly by securing additional food resources or parental investment (Dunbar 1995, Põldmaa & Holder 1997, Heymann & Soini 1999). In contrast, explaining the evolution of polyandry

for males is more difficult. Given mammalian males predisposition toward polygynous mating strategies (Andersson 1994), it seems difficult to explain why a male would restrict himself to a single female and live monogamously (Reichard 2003b). Even more puzzling, from a male-perspective, are polyandrous arrangements in which males benefit from sharing mating access and perhaps invest in helping rear another male's offspring, over monopolizing at least a single female in a monogamous setting. Among nonhuman primates, polyandry has so far only been considered relevant in the subfamily *Callitrichinae*, where more than a single male is needed to successfully rear offspring (Goldizen 1987, Digby *et al*. 2007), and in humans where it is limited to populations coping with harsh environments (Goldstein 1976, Johnson & Zhang 1991).

The occurrence of polyandry when direct paternal care is absent and outside extreme habitats is a challenging question for our understanding of the evolution of animal mating systems. In most species where it occurs, polyandry is not the sole mating arrangement between the sexes but occurs alongside monogamy, polygyny, or sometimes polygynandry, as seen in the variable mating system of tamarins (Goldizen 1987), dunnocks (Davies 1992), and some humans (Wiley 1997). In a flexible mating system, the question becomes under which specific conditions the probability of polyandry increases.

Because males usually benefit from mating with many females (Bateman 1948), advantages for males restricting themselves to mating with a single female are rare in the animal kingdom. This is

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evident in the many, if not most, pair-living birds and mammals in which extra-pair copulation (EPC) is common, *i.e.*, pair-living males mate with multiple females in addition to the female they share a territory with (Palombit 1994b, Fietz *et al.* 2000, Schülke *et al.* 2004, Akçay & Roughgarden 2007). Thus, mating exclusivity may not be a corollary of polyandrously living males. Nevertheless, polyandry is theoretically still expected to evolve when the average reproductive success of each of two (or more) cooperating males exceeds that of a single monogamous male independent of the males' opportunities for EPCs (*e.g.*, Galapagos hawk *Buteo galapagoensis* [DeLay *et al.* 1996], noisy miner *Manorina melanocephala* [Põldmaa & Holder 1997], callitrichids [Koenig 1995]). In addition, it may occur where two (or more) males combine paternal efforts. However, polyandry may also evolve in the absence of direct paternal care, for example, via cooperative territory and/or female defense. When female reproduction is restricted by resources within the boundaries of a territory, male territorial behavior (advertisement and defense) may function to attract and defend females (Carranza *et al.* 1990, Fischer & Fiedler 2001); cooperating polyandrous males may be more successful than a single male in establishing and maintaining a home range necessary for female reproduction. Seddon *et al.* (2003) suggested, for instance, that benefits of communal territorial defense were responsible for the development of polyandry in a population of the subdesert mesite, *Monias benschi*, but no such example has been found in primates so far.

In some species with a flexible mating system, a negative correlation between the number of males and their ability to control resource has been found, suggesting that costs and benefits of polyandry for males are resource dependent. When a male can control resources alone, monogamy evolves, but when two or more males are necessary to secure resources for a single breeding female, or a female range becomes so large that it cannot be defended successfully against competing intruders by a single male, polyandry emerges (Wittenberger 1980, Davies & Lundberg 1984). Work by Davies and Lundberg (1984) on the dunnock (*Prunella modularis*) has shown, for example, that polyandry develops where females live under low-quality habitat conditions while polygyny prevails when females live on high-quality territories. When habitat quality was low, female dunnocks expanded their ranges beyond what a single male could defend. The dunnock example illustrates how resource distribution can influence social systems, suggesting that social organization and mating system flexibility can be resource dependent.

Recently, a flexible mating system including monogamy and polyandry has been noted in white-handed gibbons *Hylobates lar* L. (Palombit 1994a,b; Brockelman *et al.* 1998; Sommer & Reichard 2000; Reichard 2003a, in press; Reichard & Barelli 2008). While most white-handed gibbon groups at Khao Yai conform to pair-living monogamy, which is the overwhelming social organization and mating system in the family (Fuentes 2000, Bartlett 2007), some groups were also consistently found to be polyandrous (16–42%; Barelli *et al.* 2008, Reichard & Barelli 2008, Reichard in press). Sporadically polyandrous groups have also been noticed in other gibbon species and populations (*Hoolock hoolock* [Siddiqui 1986], *Hylobates klossii* [Fuentes 2000], *H. lar* [Carpenter 1940], *H. moloch* [Malone & Okatvinalis 2007], *Symphalangus syndactylus* [Lappan

2007]) but no explanations are yet available for their formation (reviewed in Fuentes 2000).

Why the Khao Yai gibbons exhibit a flexible mating system is not yet clear, but paternal care is unlikely to account for it because males of most gibbon species including white-handed gibbons do not directly care for infants, even in the siamang (*S. syndactylus*), the only hylobatid showing substantial paternal care (Lappan 2008). This provides a unique opportunity to investigate an alternative explanation for the development of polyandry in these primates.

Gibbons are gracile arboreal Asian apes with most species weighing only 5–6 kg (Smith & Jungers 1997). They are sexually monomorphic and white-handed gibbon males and females are of light buff to brown or black pelage color. Females give birth to a single infant at a time, at long intervals of about 3.4 yr and, like all apes, they are characterized by a slow life history (Reichard & Barelli 2008). They rely heavily on the ripe fruit pulps of tropical trees and woody climbers (Chivers 1984), which they reach in swift suspensory locomotion, and live on home ranges of 17–40 ha that remain sometimes unchallenged in the possession of residents for years or even decades (Carpenter 1940, Bartlett 2007, Savini *et al.* 2008). A portion of the home range is commonly defended against conspecifics during regular intergroup encounters along small overlapping zones between ranges (Reichard & Sommer 1997, Bartlett 2007), with complex, loud calls, or songs, sung by males and females that propagate over distances of > 1.5 km (Raemaekers *et al.* 1984, Cowlishaw 1992, Clarke *et al.* 2006). Intergroup encounters involve a variety of behaviors between individuals that range from friendly cofeeding and cotravel to agonistic chases, although severe aggression is very rare (Reichard & Sommer 1997). All parts of the range are entered routinely during a relatively long day journey (Mitani & Rodman 1979) of 1–1.5 km (Chivers 1984).

In this paper, we explore links between the distribution of resources and the occurrence of polyandry in Khao Yai white-handed gibbons. We measured forest productivity of seven gibbon home ranges and tested the hypothesis that the mean number of males sharing access to a female is positively related to the size of territories. Analogous to Davies' (1992) study of dunnocks, we expected polyandry to be more prominent on poorer than on richer home ranges. Hence, we predicted a negative correlation between home range quality and home range size, because in areas of high forest productivity a small range would be sufficient to support a female. Accordingly, we predicted that small range size would be associated with monogamy, because defending a smaller range was assumed to be more easily achieved by a single male than defending a larger range. Based on the nature and locations of intergroup interactions witnessed during prior research (*e.g.*, Reichard & Sommer 1997), we assumed that mainly males defended territories in our population, which concurs with the observation that costs of territorial maintenance are generally higher in gibbon males than females (Brockelman & Srikosamatara 1984, Mitani 1987). However, since female gibbons live in all-purpose territories and mating and breeding does not occur with nonterritorial females, we do not exclude the possibility that male territorial behavior may also be interpreted as a form of mate defense. We further predicted that the probability for polyandry would increase as home ranges
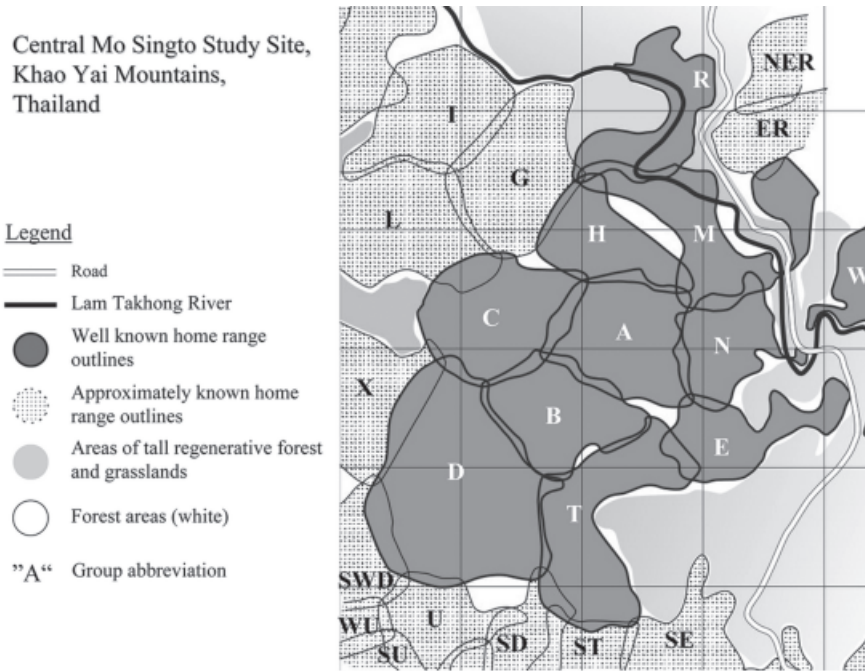
FIGURE 1. Locations of gibbon home ranges in the Central Mo Singto study site.

became larger, which would increase potential mutual benefits for cooperating males in maintaining their home range. Thus, a positive relationship between the time study groups spent in a polyandrous arrangement and home range size would occur. In this paper, we test the first part of our model, *i.e.*, a negative relationship between the probability of polyandry and territory resources. We then provide preliminary data supporting the second part of our model, namely that two males would be needed on the largest territories. However, we are aware that a final test of the latter part of our hypothesis still requires more data on intergroup encounters and social relationships between males in polyandrous groups. As an expression of the cooperative nature of polyandry, we predicted undisturbed, shared social and sexual access to the female and their participation in territorial/female defense would occur for both males. Further studies, however, are necessary to more thoroughly test our assumption of territorial defense increasing linearly with size, making it less economical for a single male to defend a large range compared to cooperating males.

METHODS

STUDY SITE AND SPECIES.—The study was conducted at the Central Mo Singto site, Khao Yai National Park, Thailand (2168 km^2; 14°26′ N, 101°22′ E; *ca.* 130 km NE of Bangkok), in slightly hilly terrain 730–890 m asl. The site covered *ca.* 2 km^2 inhabited by about 10 white-handed gibbon groups (Fig. 1) that have been the focus of research since the late 1970s (see Raemaekers & Raemaekers 1985, Reichard 1995, Reichard & Sommer 1997, Brockelman *et al.* 1998, Barelli *et al.* 2007, Savini *et al.* 2008).

Khao Yai is a seasonally wet, evergreen forest in most parts (Kerby *et al.* 2000) with a distinct dry season (November–April) followed by a wet season (May–October). In 1999–2002, average precipitation was 3483 mm (4911–2810 mm). Average daily temperature varied annually between 18.7°C and 28.3°C and humidity ranged from 64.6 percent in the dry to 77.1 percent in the wet season.

Social behavior data were collected on eight well-habituated groups (see Fig. S1; extending fig. 1 of Brockelman *et al.* 1998) for which long-term data were available. Age classes were defined as: infants, ages 0 (birth)–2 yr (age of weaning; *cf.* Treesucon 1984), partially carried by the mother (Brockelman *et al.* 1998); juveniles, 2–4 yr, of relatively small size, independent from the mother but tending to follow her closely; adolescents, 4–6 yr of age; and subadults, 6 yr–full growth (Reichard 2003a). Adults are full-grown individuals able to reproduce, which usually occurs at around 8 yr in this population.

MEASURES OF HOME RANGE SIZE.—Outlines of group home ranges were produced from daily night-tree to night-tree follows. Travel data were collected by continuously transcribing the movements of an observed group on a detailed trail map carried in the forest. Daily travel records varied between study groups (A: $N = 117$ d; B: $N = 98$ d; C: $N = 130$ d; D: $N = 86$ d; H: $N = 135$ d; R: $N = 116$ d; and T: $N = 137$ d). The size and shape of group home ranges were measured as 95 percent minimum convex polygons (see Linnell *et al.* 2001) based on all observed travel. Minimum convex polygons of groups R and T were adapted in areas where the home range bordered grassland. Minimum polygon outlines were later digitized in ARC/INFO 3.4, and the area of a polygon was

calculated using ArcView 3.0a software to obtain the actual home-range sizes. Home ranges showed negligible seasonal variation in size and remained broadly unchanged over the course of the ecological data collection period (2001–2003).

HOME RANGE QUALITY AND FOREST PHENOLOGY.—The spatial distribution of plant resources was measured on 13 20-m-wide north–south transects (total length 19.4 km, range: 620–2100 m) across seven gibbon home ranges. Thus, our study transects included 20 percent of each of the study groups' home ranges covering 39.8 ha in total. Along transects, trees > 10 cm dbh were marked, measured, and identified. A total of 19,524 individual trees were included in our analyses.

On monthly phenology walks (May 2001–September 2003), 10 individual trees for each of 31 important nonfig tree species were monitored once a month for the presence of ripe and unripe fruits, young leaves, flowers, shoots, or buds. All fig trees > 40 cm dbh found in the area (208 individuals of 16 species) were monitored twice a month. Important species were those that, combined, made a large contribution to gibbon feeding time ($\geq$ 80%) in each month of the study (Savini *et al.* 2008). Abundance was estimated on a relative 0–4 point scale, with 0 representing the absence of a given plant part and 4 scoring the full presence in a crown. All fig species were monitored twice a month because figs can have reproductive cycles shorter than a month.

Home-range quality was defined as the monthly productivity per ha in each home range. Productivity calculations included all consumed important species identified during a 2-yr monitoring period prior to the onset of phenology walks. Our productivity measures combined the measure of food abundance (*FAI*) with a biomass coefficient (*b*), which included relative fruit load (see Savini *et al.* 2008).

TERMINOLOGY: SOCIAL ORGANIZATION AND MATING SYSTEM.—A group was defined as polyandrous when two adult males were present with one female and both were believed to be unrelated to the female based on social histories, thus representing potential sexual and breeding partners. We distinguished from polyandrous groups those groups in which an adult son of the female was present. For these groups we used the simple term 'multimale group', which makes no assumptions about potential mating relationships. As the aim of our analysis was to define the role of a second adult male in territorial/female defense, we started our analyses by considering the function of a matured male offspring or an additional unrelated male. Finally, we identified groups as monogamous when there was only one adult male present with a female and the male was not known to maintain sexual relationships with females other than the female he shared the home range with.

DATA COLLECTION.—Demographic data on eight groups (group J was excluded from the ecological analysis) were available from January 1993 until December 2006 (Fig. S1). Behavioral data of adult members of three polyandrous groups (D, J, and T) were collected during most months from August 2003 until February 2005 for a total of 525 d. Data were only included when study groups were observed for at least 5 d/mo (D: 202 d; J: 192 d; T: 131 d) except for data on dueting, where we used the total number of duets available throughout August 2003–February 2005. The observation time for group T was divided into two periods, because the female's primary partner changed during the study (August 2003–April 2004; and June 2004–February 2005; for status assignment see below). Five trained field assistants collected behavioral and proximity scan sample data at 5-min intervals for adult group members (Martin & Bateson 1993). Social grooming and singing activities were noted for focal animals as continuous records. Instances of sexual interactions (copulations) and aggression within and between groups were collected as all occurrence data. Observations usually started before dawn when the gibbons were still in their night trees and ended after animals had entered a night tree in the late afternoon. To reduce potential biases due to following a single individual, observation targets were rotated each day.

MALE STATUS IN POLYANDROUS GROUPS.—We distinguished two classes of males in polyandrous groups based on behavioral interactions among adults. The male that shared less than two-thirds of a female's interaction frequencies was identified as her primary male partner, and any other males were considered secondary partner(s). Identification of male status across study groups followed detailed behavioral observations of three representative polyandrous study groups. We used: (1) participation in duet singing; (2) social grooming; and (3) sexual interactions as measures of male involvement with a female, and where available also included agonistic interactions in our assessment. An important component of status assignment was duet singing, because, in polyandrous groups, females only engaged in duets with the primary male partner.

STATISTICAL ANALYSES.—Productivity variation among home ranges was tested with an analysis of variance (ANOVA) for which sphericity for repeated measurement was controlled. To evaluate differences in home-range productivity between groups we compared monthly productivity scores with an ANOVA with repeated measurements. By using a within group/repeated measurement design, we matched the scores of groups within each month. Pairwise comparisons followed significant results. We verified the assumption of normality by visual inspection of the data using QQ-plots. The assumption of sphericity was verified by evaluating Greenhouse Geisser's ε (Howell 2002). In case of a nonlinear relationship or nonnormal data distribution, we used Spearman rank correlations. We used Pearson's partial correlation to describe the relationship between two variables (*e.g.*, A and B) while keeping a third variable (*e.g.*, C) constant. All tests were two-tailed with an α error level of 0.05. Means and standard deviations are presented throughout the text. Statistical testing was run on SPSS release 11.0.

RESULTS

HOME RANGE SIZE AND QUALITY.—Large variation in home range size between gibbon groups was recognized (Table 1). Average home range size was 27.9 $\pm$ 11.25 ha (*N* = 7). Group R had the smallest

TABLE 1. *Home range size, productivity, neighbors, and polyandry in white-handed gibbon groups (n.a. = not available; y = years; mo = months).*

Group	Home range Size (ha)	Home range Productivity (kg/ha)	± SD	Demography observation (yr)	Two adult male (% time)	Multimale groups (% time)	Polyandrous group (% time)	(n)	Neighboring groups
A	30.4	482	396	13	48.7	30.1	18.6	6	B, C, E, H, M, N
B	23.8	394	604	13	24.4	1.3	23.1	4	A, C, D, T
C	25.6	421	457	13	60.9	60.3	0.6	7	A, B, D, G, L, H, X
D	49.7	158	148	9.67	100.0	11.2	100.0	7	B, C, T, U, SD, SWD, X
H	20.7	341	281	13	40.4	40.4	0.0	5	A, C, G, R, M
J	n.a.	n.a.	–	7.17	47.7	0.0	47.7	5	L, O, Q, NQ, NJ
R	14.8	855	450	12.83	25.3	24.7	0.6	3	M, H, G
T	31.1	326	336	7.08	54.1	0.0	54.1	6	B, D, E, SD, ST, SE

home range covering *ca.* 14.8 ha whereas the largest range was of group D's, more than three times the size of group R and covering *ca.* 49.7 ha.

Annual productivity (June 2001–September 2003) varied across home ranges ($F_{6,66}$ = 6.062, P < 0.001; SD values reflect annual variation in productivity over 2.5 consecutive phenology years; Table 1). Significantly lower productivity, compared to all other groups, was found in home range D ($P \leq$ 0.05; average 158 kg/ha, range 579–0.1 kg/ha/mo, N = 29 mo) whereas highest productivity occurred in group R's home range ($P \leq$ 0.05; average 855 kg/ha, range 1808–0.5 kg/ha/mo, N = 29 mo). Of the remaining five groups only group T's home range productivity was significantly lower than that of groups A and C (Table 1). Overall, a negative linear relationship between productivity and home range size was detected: as productivity per hectare decreased, home range size increased (r = −0.761, df = 5, P = 0.047; Fig. 2).

SOCIAL VARIATION AND HOME RANGE SIZE.—The relationship between home range size and time spent with more than one adult male was significantly positive (r = 0.964, N = 7, P = 0.001). As home ranges became larger, the probability of time spent with more than one adult male likewise increased (Fig. 3A). This relationship

remained significant when mature sons were removed from the data set and only polyandry with males unrelated to a breeding female was tested (r_s = 0.879, N = 7, P = 0.009; Fig. 3C). In contrast, multimale periods exclusively related to the presence of an adult son and home range size were not significant (r_s = −0.357, N = 7, P = 0.743; Fig. 3B). We also tested the possibility of home range quality being a confounding variable in the analyses of the relationship between home range size and group composition. The result of the partial correlation testing for a relationship between home range size and time groups spend polyandrous while controlling for home range quality was significantly positive (r = 0.927, N = 7, df = 4, P = 0.028). Therefore, we assumed that home range quality was not a confounding variable in our analysis of home range size and group composition.

DEVELOPMENT AND DYNAMICS OF POLYANDROUS GROUPS.—Between January 1992 and December 2005 (13 yr) multimale and polyandrous groups developed 16 times in seven groups (Table S1). Two distinct pathways were noticed: first, pair-living groups became multimale eight times because a female's son had matured. Of these, five males later dispersed, but three delayed dispersal and were still resident in their natal groups at the end of data collection.
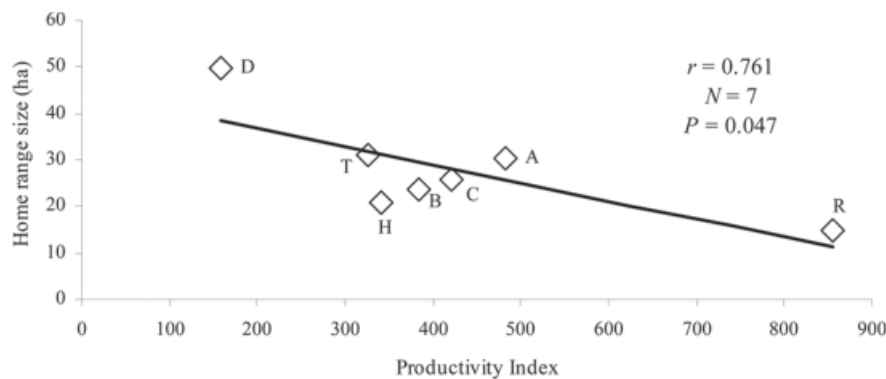

FIGURE 2. Forest productivity versus home range size in the white-handed gibbon population at Khao Yai National Park.
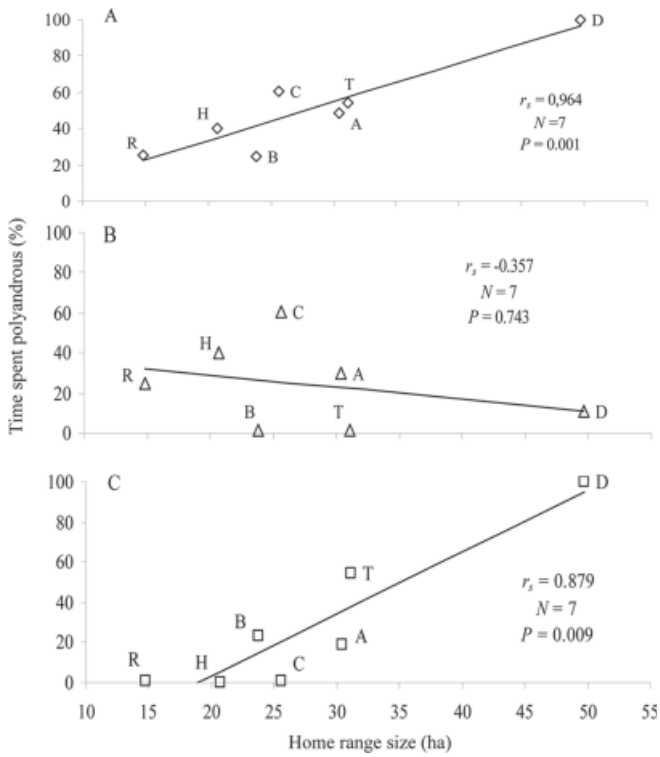
FIGURE 3. Relationship between gibbon home range size and time spent polyandrous for males unrelated to a resident female.

Second, polyandry developed another eight times via an adult male's immigration. Three short ($\leq$ 1 mo) periods with more than one male occurred after a male immigration because the immigrant rapidly replaced the resident male as the female's primary partner and ousted the former resident male resulting in a simple male takeover. Five times stable polyandry developed (range: 6–45 mo). Of six immigrant males of known origin, four were recently matured, previously unpaired neighboring males, whereas two were mature, previously paired males, one of which had been replaced elsewhere immediately prior to immigration (Table S1).

Of the eight immigrant males, six quickly took over the primary position from the resident male as indicated by dueting, grooming, and more frequent copulation with the female, whereas two immigrants became a secondary partner (Tables 2 and S1; one achieved primary status later). Only one initially secondary immigrant partner later became a female's primary partner (group T). Finally, two secondary males later left polyandrous groups during the observation period.

SOCIAL RELATIONSHIPS IN POLYANDROUS GROUPS AFTER A MALE IMMIGRATION.—Detailed behavioral observations are available for three groups that experienced male immigration to illustrate patterns of adult relationships in polyandrous groups. An asymmetrical distribution of social interaction and copulations emerged (Table 2). In all three groups, only one male sang duet songs with the female, a pattern likewise observed in other polyandrous groups. Agonistic

TABLE 2. *Status and socio-sexual interactions of males with females in three polyandrous white-handed gibbon groups, Khao Yai National Park, Thailand.*

Group	Behavior observation time (days)	Female reproductive status§	Duet singing with female (N) 1°	Duet singing with female (N) 2°	Aggression (N) within-group 1°	Aggression (N) within-group 2°	Aggression (N) between-groups 1°	Aggression (N) between-groups 2°	Aggression (N) 1° & 2°	Social grooming 1° with female min	Social grooming 1° with female %	Social grooming 2° with female min	Social grooming 2° with female %	Social grooming 1° and 2° min	Social grooming 1° and 2° %	Copulation 1° N	Copulation 1° %	Copulation 2° N	Copulation 2° %
D	202	pr, lc¹, cy, pr, lc	345	0	2(c), 1(d)	1(c)	1(c), 1(t)	–	2(c)	3584	73.0	400	8.2	925	18.8	70	88.6	9	11.4
J	192	pr, lc², cy, pr	163	0	1(b), 9(c), 1(d), 13(t)	–	1(b), 39(c)	20(c)	1(b), 1(c)	3634	72.0	1410	28.0	–	–	76	86.4	12	13.6
T³	58	Lc	53	1	1(b), 11(c), 1(t)	–	1(b), 5(c), 1(t)	3(c), 1(t)	–	1526	68.6	699	31.4	–	–	–	–	–	–
	73	lc, cy	90	0	–	–	1(c)	1(c)	–	981	86.2	157	13.8	–	–	3	100	0	0

1° = primary male; 2° = secondary male; § = estimated for the observation period from previous birth; pr = pregnant; cy = cycling; lc = lactating; ¹ = infant lost after 3 wk; ² = infant lost after 2 wk; ³ = primary male changed (first period August 2003–April 2004; second period May 2004–February 2005); "–" = not observed; (b) = bite; (c) = chase; (d) = displace; (t) = threat; * = significant variation between males (P < 0.05).

interactions between males were rare, but both participated in territorial defense and, in the case of group D, developed a reciprocal social grooming relationship (Table 2).

DISCUSSION

Our analyses of seven gibbon home ranges in the Central Mo Singto study area revealed a negative relationship between forest quality and home range size: larger home ranges contained fewer resources. The length of time groups were polyandrous after a male immigration showed a significant positive relationship with home range size, but not when a son had matured on a parental home range.

The starting point to understand shifts from pair-living to cooperative polyandry in Khao Yai gibbons is likely the observed negative relationship between forest quality and home range size (Fig. 2). A similar relationship has been suggested by Adams (2001) and has been verified in various animals (e.g., dunnocks [Davies & Lundberg 1984], pileated woodpecker [Renken & Wiggers 1989], roe deer [Tufto et al. 1996], mule deer [Relyea et al. 2000]). Davies and Lundberg (1984) have also shown that large female home range size was associated with polyandry and shifted toward monogamy in areas with denser resource distributions that would allow females to live on smaller home ranges.

Interestingly, in our sample the smallest home range of highest productivity (group R) was located on both sides of a river with a year-round water supply (~720 m asl). In contrast, the largest range (group D) was furthest away from the river with a northeastern border alongside the top of a gentle ridge (820–860 m asl) and a long, SSW-facing, dry slope of comparatively low resource quality. Group T, with the second-largest home range, shared parts of this ridge and dry slope (Fig. 1). It seems plausible that topography influenced forest productivity, which in turn may have affected the probability of gibbon polyandry formation. However, it is important to note that additional social factors were also responsible for polyandry in our population, as groups in areas without particular geographic features were likewise polyandrous. This becomes understandable when individual benefits and costs from developing polyandry are considered.

BENEFITS AND COSTS OF POLYANDRY FOR FEMALES.—It is widely recognized that access to food resources limits reproduction in mammalian females (Sterck et al. 1997). Thus, gibbon females could suffer increased feeding competition from the continuous presence of a second adult male on their territory. This argument seems unlikely, however, because in another study (Savini et al. 2008), we were able to show the absence of significant variation in reproductive success for seven Khao Yai females that already obtained a breeding position despite significant variation in social structure and home range size. Females apparently compensated living in comparatively lower quality forest patches with an increase in range size (Savini et al. 2008). The idea that female gibbons may benefit from polyandrous mating is further supported by the recently described sexual swellings of white-handed gibbon females that are similar in function to exaggerated anogenital swellings of many

cercopithecine primates and chimpanzees (Barelli et al. 2007), as well as their widespread polyandrous mating behavior (Barelli et al. 2008, Reichard in press). In short, females seem to either be neutral toward or favor a polyandrous arrangement, suggesting that polyandry in the study population may primarily depend on cost-benefit considerations for males. This does not mean that the role of females in promoting or avoiding polyandry in our population is negligible, because costs or benefits of polyandry may vary for individual females depending on socioecological context. For example, for a female paired with a 'good quality' male, it may be more advantageous to live in a stable monogamous structure rather than polyandry, because a struggle for dominance between males could lead to social instability, which may negatively impact her reproduction, or because mating with more than one male may increase the risk of contracting sexually transmitted diseases (Nunn et al. 2000). In contrast, a female paired with a 'low-quality' male may actively promote polyandry to gain increased resource access and/or better genes for her offspring (Yasui 1997).

COSTS AND BENEFITS OF POLYANDRY FOR MALES.—Behavioral data of polyandrous trios indicated a status difference between adult males. Females' primary partners were identifiable as the males who dueted with females and shared the larger portion of social grooming and copulations (see also Barelli et al. 2008). Primary male partners were also able to elicit signs of subordination, such as submissive vocalizations and facial expressions, from secondary male partners in competitive situations, although overt aggression was rare (Table 2) and too infrequent to be used as a reliable indicator of male status.

Demographic data from Khao Yai suggest that polyandry primarily results from immigration of recently matured neighboring males (Table S1). In most cases, young immigrant males established themselves as a female's primary partner within days or weeks, and females accepted, or perhaps even supported, the postimmigration male status change with a rapid shift of their social attention to the immigrant male. Females were not seen to resist duet calling, grooming, or copulation attempts, or to have had other difficulties with immigrant males. However, polyandry did not always develop after a male immigration because immigrants not only took over the primary position with the female but sometimes also ousted the former resident male, resulting in a rapid male change without a shift from monogamy to polyandry.

HOW A PRIMARY MALE MAY BENEFIT FROM THE PRESENCE OF A SECONDARY MALE?—Given the potential for ousting a resident male, why would an immigrant who attained primary male status tolerate a secondary male? Davies (1992) recognized for the dunnock a male hierarchy in polyandrous trios. The subordinate male could only copulate when the female escaped the dominant male's control and no social interactions between males were observed. However, such 'opportunistic' polyandry—resulting partly from a female inhabiting a large home range that overlapped substantially with the smaller ranges of two separate males—differed from polyandry in gibbons because gibbon males share a home range and immigrants seem capable of ousting a secondary male. Hence, a logical interpretation of the gibbon scenario must assume that males cooperate

in some form and that under certain circumstances primary males benefit from the presence of a second male. Alternatively, polyandry could also develop because the cost of confronting another male may be outweighed by accepting the male. We suggest that secondary males possess some leverage (Lewis 2002) that can tip the cost-benefit balance for a primary male toward tolerating a secondary male. This interpretation is indirectly supported by the absence of frequent intragroup aggression, meaning that males in polyandrous gibbon groups did not try to evict each other (Table 2).

The service a secondary male may provide is aid in territory/female defense. In the subdesert mesite, for example, males engage in communal singing at range borders and chase away intruders; communal territorial defense may become more important as range size increases, which promotes the development of cooperative polyandry in these birds (Seddon *et al.* 2003). A similar relationship may exist in our population where polyandry prevails longer on larger ranges. We hypothesize that larger home ranges require higher investment in territorial defense due to increased patrolling, for example, as contested areas between home ranges increase in size stemming from increased travel, then increased intergroup encounter frequencies rise from the presence of more neighboring groups and longer shared borders. We presently lack firm quantitative data to broadly test this idea, but found in accordance a tendency for groups with larger home ranges to have more neighbors (Table 1); significantly longer daily travel was confirmed in the polyandrous group living in the largest home range (group D; Savini *et al.* 2008). Indirect support for the hypothesis also comes from the observation of participation of secondary males in territorial disputes, which in contrast was rare to absent by grown-up sons in multimale groups.

Alternatively, our data (Fig. 3) may also be interpreted as evidence that secondary males provided female defense to primary males against outsiders. Assuming that dispersal costs and benefits for adult sons would equal investing into securing resources for kin as much as resource defense would benefit a secondary male, it becomes difficult to explain why natal sons would not participate in intergroup encounters. Given grown-up sons' kin relationships with their mothers and siblings, they are expected to invest at least as much in territorial resource defense as an unrelated secondary male would. Our behavioral data were inconsistent with this expectation, suggesting that the principal support secondary males may provide to primary males lies with female defense.

Similarly, an important potential benefit to tolerating a secondary male may be related to direct mate guarding of a female from outsiders when she is in estrus. Recent field studies indicate that gibbon females engage in EPCs(Palombit 1994b; Reichard 1995, in press; Barelli *et al.* 2008), although only in the absence of a resident male (Reichard 1995, 2003b). Hence, a secondary male that can provide extra guarding against EPCs may benefit a primary male, who overall has more control over the resident female's sexual activity (Table 2). A final benefit could be an increase in the tenure length of a primary male. This is difficult to test, however, because the idea of a male tenure is novel to gibbon studies and therefore adequate data have been collected thus far. Nevertheless, we can explore the underlying logic of the argument with our long-term demographic data. First, group composition changes due to immigration are frequent in the saturated Khao Yai habitat (Reichard, in press). Second, documented male immigrations have so far occurred in pair-living groups but not polyandrous trios, except once (group A) when a male immigrated into a polyandrous group where the two resident males were believed to be his brother and father. Third, most male immigrations have led to a male status change, *i.e.*, pair-living males became a female's secondary male partner or were ousted. These observations suggest a considerable positive influence of the presence of a secondary male for a primary male's tenure when challenged with the unpredictable risk of male immigration attempts.

POTENTIAL COSTS OF POLYANDRY FOR A PRIMARY MALE.—The key cost to a primary male for accepting polyandry is lost paternity. This cost may be substantial because on high-quality, small home ranges we found that immigrant males were always intolerant, *i.e.*, behaving consistently agonistic toward the other male involving threats, chases, and occasionally contact aggression, and always ousted the resident male. It appears that the balance between pair-living or becoming multimale is delicate. Presumably, on a small range, a single male can successfully defend resources and the female alone, and thus the presence of a secondary male may not be worth the cost of shared mating.

Another cost to a primary male may arise from the additional energy expenditure required to control a secondary male's access to the female and to prevent a male status reversal. We consider these costs marginal, because gibbon groups are spatially cohesive, suggesting that no additional energy expenditure would be needed to supervise a second male, and polyandry that rests upon mutual male cooperation would reduce potential status reinforcement costs. Repeated agonistic interactions between males can be expected to become negligible after male status has initially been settled, which would, for example, minimize negative effects of physiological stress responses. Our social behavior data support such interpretation, because within-group male aggression was rare and, at least in one study group, grooming was observed between the males. The latter may be an effort to reduce tension or an expression of a stronger social bond between these males, perhaps because of the primary male's greater need of support. Alternatively, social grooming may also have been a strategy of the primary male to better control the secondary males' behavior.

BENEFITS AND COSTS FOR A SECONDARY MALE TO STAYING IN A POLYANDROUS CONSTELLATION.—Secondary males sometimes copulate with the group female (Barelli *et al.* 2008; Table 2) providing them with a chance of reproduction. In a study of ovarian cycles of females in our population, Barelli and colleagues (2007) were able to show that in one polyandrous group a secondary male copulated on a female's calculated day of ovulation.

Staying in a polyandrous group may have additional advantages. Similar to mature sons delaying dispersal, a secondary male may also await better reproductive options from the safety of a known home range, for example a reproductive opening or a chance to take over a nearby home range and female. Such a pattern was

observed in groups B and T (Table 1) in our sample, where the secondary male replaced a neighboring male after a female immigration. Another way of awaiting better reproductive options would be to wait for a chance of status reversal, a pattern likewise observed once during our data collection.

Finally, secondary male status may be beneficial as a way to avoid being a floater (Crespi & Ragsdale 2000). Mitani (1990) concluded that mortality was highest in dispersing subadults in his study of agile gibbons. In our population, solitary life appeared to be similarly associated with potentially high costs, as solitary individuals were rare. The mean annual proportion of solitary individuals was 2.5 ± 3.2 percent (range: 0–8.3%) of social units surveyed during 1992–2005 (N = 253 social units; Reichard in press). Solitary life is presumably associated with the lowest reproductive potential for a gibbon male, as territorial residency has been claimed to be a prerequisite for successful reproduction in our population and others (Leighton 1987, Palombit 1999). Even reported EPCs in gibbons involved paired males and not floaters (Palombit 1994a,b, Reichard 2003a, Barelli et al. 2008).

For secondary males, direct benefits from polyandry may be small as chances for their own reproductive success or accomplishing a status reversal are probably low. Thus, an important incentive for secondary males to remain in a polyandrous group may be to avoid potentially high costs of floating between established home ranges.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Polyandry in selected Khao Yai white-handed gibbon groups, January 1992–December 2005*

FIGURE S1. Social histories of eight white-handed gibbon groups, Central Mo Singto, Khao Yai 1993–2006.

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