

# Group Composition and Monandry in Grizzled Langurs, *Presbytis comata*, on Java

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**Abstract:** Grizzled langurs, *Presbytis comata*, a largely sexually monomorphic species, are reported to occur in populations where either the majority of groups comprise 1 adult male with 1 adult female, or where groups comprise 1 adult male with multiple females. As such, they may have a monandrous mating system. I investigated whether 1-male/1-female groups indeed form a significant part of the species' social system, and whether habitat variation (forest fragment size, distance to the forest edge, altitude) affects social organization. I found the species from sea level to 2,565 m above sea level in groups from 1 to 13 individuals. I recorded mostly 1-male/multifemale groups with offspring or, alternatively, all-male groups. Two out of 55 groups comprised 1-male/1-female groups with offspring. Group size was negatively correlated with altitude and forest fragment size, and positively correlated with increasing distance from the forest edge. Altitudinal variation in group sizes was driven mainly by fewer adult females being present in groups at higher elevations; the number of adult males (almost invariably 1), subadults, juveniles, and infants, as well as the infant/adult female ratio, showed little altitudinal variation. One-male/1-female groups have been recorded repeatedly over a 25-year period in a high-altitude population on Mt. Patuha, West Java, but even here, on average, three fifths of the groups comprise 1 adult male with multiple females. At high-altitude sites, *P. comata* may indeed have a monandrous mating system, but at lower elevations it seems similar to that of other *Presbytis* langurs.

## Introduction

The genus *Presbytis* sensu stricto comprises a group of arboreal colobines found in the Indomalayan region, from southern Thailand, south to Sumatra, Java and Borneo and smaller off-lying islands. Over the last 3 or 4 decades, partially aided by molecular phylogenetic analysis [Meyer et al., 2011; Vun et al., 2011] and partially by adopting different species concepts [Groves, 2001], the number of species has increased from 8 [Davies and Oates, 1994] to 17 [Zinner et al., 2013]. While Bennett and Davies [1994] concluded that differences in socioecological behaviour in *Presbytis* langurs appear to be due to differences in habitat rather than to intrinsic differences between species, when group size, morphology and antipredator behaviour are taken into account, the genus can be divided into 3 distinct groups [Nijman and Nekaris, 2012]. First are the ones that live primarily in large groups, comprising 1 or 2 adult males with several adult females plus offspring, and that are typically brightly coloured and vocal when disturbed (e.g., banded langur, *P. femoralis* [Curtin, 1980]; red langur, *P. rubicunda* [D'Agostino et al., 2016]). Second are those species that live in smaller 1-male/multifemale groups, where individuals are typically bicoloured and that are less vocal when disturbed (e.g., Hose's langur, *P. hosei* [Nijman, 2010], or Thomas's langur, *P. thomasi* [Steenbeek and Assink, 1998]). Third are species that live in 1-male/1-female groups, and where individuals are dark in colour and that rely on crypsis as an antipredator strategy (e.g., Siberut langur, *P. siberu* [Tilson and Tenaza, 1976]). The available data for at least 1 species, the white-fronted langur *P. frontata*, is suggestive of a monandrous social organization (sensu Tenaza and Fuentes [1995]) i.e., 1-male/multifemale and 1-male/1-female groups coexist in a single population<sup>1</sup> [Nijman and Nekaris, 2012]. Too few data are available for a number of species regarding their socioecology to make firm conclusions (e.g., Natuna langur, *P. natunae* [Lammertink et al., 2003; Nijman and Nekaris, 2012]), or there are conflicting reports or apparent differences in interpretation concerning a species' social organization. The latter is the case for *P. comata*, the grizzled langur from Java.

Based on data collected in 1976–1977 by Ruhiyat [1983, 1991] at 1 of 2 sites in western Java (i.e., Telaga Patengan, also known as Situ Patenggang; Telaga and Situ meaning Lake in Bahasa Indonesia and Bahasa Sunda, respectively), *P. comata* is sometimes cited as one of relatively few monogamous Old World monkeys [Watanabe, 1981; Lott, 1991; Davies and Oates, 1994; Yeager and Kool, 2000]. Ruhiyat [1983, 1991] never mentions monogamy, but four 1-male/1-female groups with offspring, alongside two 1-male/multifemale groups, were present at Telaga Patengan during the 14-month study period. Others consider *P. comata* to occur in 1-male/multifemale groups with offspring [Leutenegger, 1982; Sterck, 2012; Zinner et al., 2013], again largely based on data collected by Ruhiyat [1983, 1991], but this time from his second study site Kawah Kamojang (Kamojang Crater). At Kawah Kamojang, six 1-male/multifemale groups but no 1-male/1-female groups were present over the 24-month study period [Ruhiyat, 1983, 1991].

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<sup>1</sup> The term “monandry,” from the Greek *monos*, “alone,” and *andros*, “man,” in zoology refers to a pattern of mating in which a female has only 1 mate at a time. In primatology, Ansel and Talmage-Riggs [1977], Roldan and Gomendio [1995], Dixson [1995], and Trevithick [1997], amongst others, used the term “monandry” to refer to females mating exclusively with 1 male in either each sexual cycle or throughout their lifetime, but Tenaza and Fuentes [1995, p. 306] redefined monandry as “a mating system in which the breeding group consists of 1 adult male and 1 or more adult females plus their young, such that the population of breeding groups consists of a mixture of monogamous and polygynous families.”

Reviewing the evolution of social monogamy in mammals, Lucas and Clutton-Brock [2013] found that male-biased sexual dimorphism is found in only about half of the socially monogamous species and that social monogamy only evolved in species in which females are at least as large as males. In primates, Opie et al. [2013] found evidence for linked evolution between social monogamy and discrete female ranging patterns (with little overlap between females), biparental care, and risk of male infanticide. In the approximately 150 species of Old World monkeys, the group to which *P. comata* belongs, social monogamy has been reported, often with mixed evidence, in De Brazza's monkeys (*Cercopithecus neglectus*) and *P. siberu*, whereas monandry has been reported in *P. frontata* and the simakobu *Simias concolor* [Watanabe, 1981; Leutenegger and Lubach, 1987; Tenaza and Fuentes, 1995; Nijman and Nekaris, 2012]. Sexual dimorphism is pronounced in *C. neglectus* and *S. concolor*, but not in *P. frontata* or *P. potenzi*; extensive range overlap is present in *C. neglectus* and *P. potenzi*, but not in *S. concolor*, and direct evidence of infanticide is lacking for all 4 species.

Here I present data on the group sizes, group composition and support for a monandrous social system in *P. comata* based on an island-wide survey and a review of the available literature. I test 4 explicit hypotheses: (1) group sizes and group composition in *P. comata* vary, but this is not related to altitude, forest area or distance to the forest edge; (2) all-male groups and solitary males, if present, show a similar ranging pattern to that of 1-male/multifemale groups; (3) 1-male/1-female groups, if present, show a similar ranging pattern to that of 1-male/multifemale groups; (4) *P. comata* groups that form polyspecific associations with other primates, if any, are similar in size to 1-male/multifemale groups, and they show a similar ranging pattern.

## Methods

### *Study Species*

*P. comata* is endemic to the western part of the island of Java, Indonesia [Nijman, 1997b; Groves, 2001] and is listed as Endangered on the IUCN Red List [Nijman and Richardson, 2008]. It is an arboreal species and as such is confined to tall forest that remains scattered along the island. Brandon-Jones [1997] recognizes the eastern populations, or at least those on Mt. Slamet and Mts. Dieng, as a separate species (*P. fredericae*). Following Nijman [1997a], Groves [2001], and Zinner et al. [2013], I consider the western and eastern populations conspecific.

There is very little sexual dimorphism in *P. comata*, either in body mass or body size measurements (Table 1). In terms of head-body length, tail length, total length, ear size, canine length and molar size, males are, on average, 2.3% (range 0.7–5.2%) larger than females, but none of these differences is statistically significant (Student *t* test, all  $t > 1.44$ , all  $p > 0.160$ ). Male feet are 10.5% longer than female feet, but this difference is not significant either ( $t = 2.14$ ,  $p = 0.064$ ) (Table 1). Data presented by Smith and Jungers [1997], based on an unpublished 1976 thesis from the Anthropological Institute in Zurich, suggest a slightly reversed sexual dimorphism with females being 0.4% heavier than males (Table 1). However, the provenance of the animals on which this is based is not known and, importantly, they were listed as *P. aygula* in the 1976 thesis, meaning that they could refer to *P. comata*, *P. hosei* (from Borneo), *P. thomasi* (from Sumatra), or a combination of these taxa (data for *P. hosei* and *P. thomasi* in Smith and Jungers [1997] were obtained from a different unpublished thesis). None of the adult wild-caught specimens in the collections of the zoological museums in Leiden (the Netherlands), London (UK), Cibinong (Indonesia), and Singapore I have examined had data on body mass associated with it.

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**Table 1.** Physical characteristics of grizzled langur (*Presbytis comata*) males and females, present- ing mean  $\pm$  SD and sample size

Measurement	Males	Females	Source
Body mass, kg	6.68 (4)	6.71 (6)	Smith and Jungers, 1997
M1 molar, mm	57.3 $\pm$ 1.6 (8)	56.4 $\pm$ 1.2 (8)	Willis and Swindler, 2004
Canine length, mm	58.6 $\pm$ 1.7 (8)	57.5 $\pm$ 1.0 (8)	Willis and Swindler, 2004
Head-body length, cm	49.7 $\pm$ 5.0 (18)	49.2 $\pm$ 7.7 (14)	
Tail length, cm	64.9 $\pm$ 6.3 (18)	61.7 $\pm$ 6.3 (14)	
Foot length, cm	17.2 $\pm$ 0.9 (7)	15.5 $\pm$ 1.5 (3)	
Ear size, mm	29.6 $\pm$ 1.5 (5)	29.4 $\pm$ 3.4 (5)	

Data are from collectors' measurements of wild-caught, adult individuals in the collections of the zoological museums in Leiden (the Netherlands), London (UK), Cibinong (Indonesia), and Singapore, unless indicated otherwise.

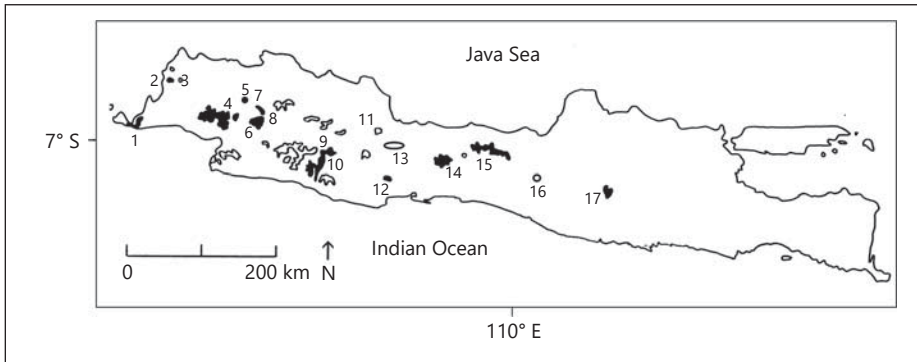
### Study Areas

The island of Java (126,500 km<sup>2</sup>), Indonesia's cultural, political and economic centre, is one of the most densely populated areas in the world. The provinces of Banten, West Java, and Central Java, i.e., the area where *P. comata* is found, has a human population of over 90 million, at a density of 1,200 people km<sup>-2</sup> (data from 2015 [BPS 2017]). Java is largely deforested, and most of the remaining forest fragments cover (parts of) the numerous volcanoes on the island. Once the island was probably completely covered by tropical forest, but its destruction dates back several centuries, probably to the 10th century AD [Whitten et al., 1996]. In effect most of the lowland forest has been replaced by a mosaic of cities and villages, agricultural land, cash crop plantations, and forest plantations, rendering the natural forest areas, and the primate populations in them, into habitat islands [Nijman, 2013].

Between the 4th and 14th century AD, Java was ruled by Hindu-Buddhist kingdoms, and from the 16th century onwards Islam became the dominant religion on the island. At present more than 90% of the people living in Java are Muslims. Primates are considered haram (forbidden to be eaten) under Islamic tenets, and hunting of primates for food is far less of an issue on Java than it is in other parts of Indonesia (including, for instance, the Mentawai Islands from where Tenaza and Fuentes [1995] reported *S. concolor* to be monandrous). On Java, primates are captured to meet the demand for the pet trade, but this is less of an issue for *P. comata* than it is for species such as slow lorises (*Nycticebus* spp.) or macaques (*Macaca* spp.), possibly because the langur is very difficult to keep alive in captivity. Support for this has recently been reported by Nijman et al. [2016] who documented the trade of approximately 2,500 primates in Java and Bali, of which only 2 or 3 were *P. comata*.

### Data Acquisition

Over the period of 1994–2013, I conducted a survey covering all major large forest areas in Java, during which *P. comata* was studied in 12 forest areas for a total of approximately 340 days inside the forest (Table 2). The study sites cover the species' entire distributional and altitudinal range (Fig. 1). Groups were located by means of transect walks in the forest or from vantage points overlooking the forest. Almost all groups were unhabituated allowing generally only brief observations, although in some situations (e.g., while seated at watchtowers overlooking the forest) groups could be observed at ease. The best counts were obtained when a group crossed a gap, including small streams or forest trails. As much as possible, groups were counted several times, but are included only once in the analysis. I identified groups either by recognizable individuals or, given that the species have stable home ranges and are territorial, by matching observations [Chapman and Chapman, 2000]. Group ranges are typically stable over time and, especially in the smaller forest areas where few groups were present, it was possible to recognize different groups over time.



**Fig. 1.** Global distribution range of grizzled langur *Presbytis comata* on Java, Indonesia. Study areas are indicated in black (together with their study area numbers). Other sites where the species is found are marked and, where they are numbered, the numbers refer to sites mentioned in Tables 2 or 4.

Despite the low degree of sexual dimorphism (Table 1), in the field males appeared slightly more robust than females, and adult females could often be sexed by protruding nipples and/or the presence of dependent young. Age classes were identified on the basis of relative size and pel- age coloration. Group counts were grouped in 3 classes: (i) known group composition, i.e., number of adult males, adult females, subadults of either sex, juveniles, and neonates; (ii) complete counts, i.e., the total number of individuals without records of all the age and/or sex classes; (iii) minimum counts, where a certain number of individuals was observed, but where in all likelihood the actual number was greater.

A group of *P. comata* and 1 or more other primate species was considered polyspecific if individuals of the respective species remained in close proximity (less than approx. 10 m) for a prolonged period (>1 h), showed spatial overlap, and if individuals of the different species clearly interacted with each other, either by simultaneous vocalizing, feeding or travelling together.

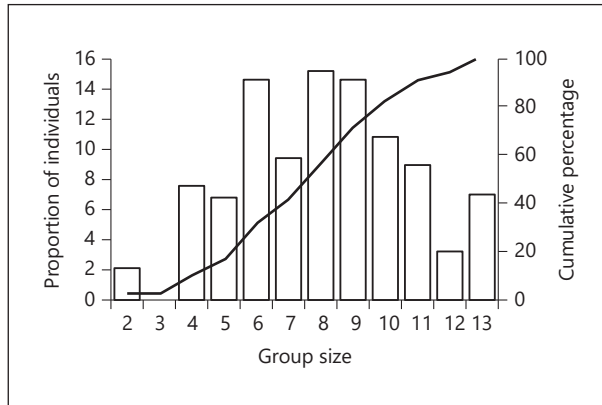
For each group I recorded the following variables: (i) altitude, recorded with a wristwatch altimeter or GPS, accurate to the nearest 50 m; (ii) estimated distance of the group in the forest interior to the nearest forest edge; (iii) longitude-latitude, recorded with a GPS or taken from forestry maps. For multiple sightings of the same group the estimated centre point of their range was taken. Each record, furthermore, received a climate score, based on the number of rainy days received during the driest 4 consecutive months of the year. These data were taken from Van Steenis [1972]. The dry season is defined as the months June to September, the remaining months comprise the wet season [RePPPOT, 1990]. Rainfalls in areas where *P. comata* was recorded range from a mean of 20–50 mm month<sup>-1</sup> for the dry season to a mean of 150–300 mm month<sup>-1</sup> for the wet season. Size of forest areas (in square kilometres) was taken from van Balen et al. [2001] and my own field data.

Additional data on group sizes in *P. comata* were obtained from the literature, including unpublished reports and theses. Group counts reported as part of density surveys (along transects or paths) often underestimated true group sizes and were normally not included.

### Analysis

In exploring variations between group sizes with environmental variables and in group comparisons only groups of known composition or complete counts were included. Some groups recorded during different years might have been included twice in the analysis, but these comprise only a maximum of 11% of the total (6/55) with on average 40 months between counts

**Fig. 2.** Proportion of individuals present in grizzled langur *P. comata* groups of different sizes showing that the majority of langurs live in groups of 8 or more. The line gives the cumulative percentage.



(range 14–77 months). Given the extent of deforestation on Java, there are no forest areas within the range of *P. comata* that still cover the entire altitudinal range from sea level to montane (Table 2). Hence, in exploring relationships between environmental variations, including the effect of altitude, data from all forest areas were pooled, as the alternative of within-forest comparisons was not an option for most forest areas.

Data were checked for normality, and data on forest area, altitude, and distance to the forest edge were log-transformed in order to approach a normal distribution. All analyses were checked for differences between populations east and west of 108° longitude (an arbitrarily chosen line running approximately halfway between the areas from where *P. (c.) comata* and *P. (c.) fredericae* have been described). No significant differences were found, and thus no further distinction is made between the western and eastern regions.

After checking for colinearity between data, a simple linear multiregression model was used to select the best subset of variables that could explain the observed variation in group size (for all statistical procedures, see Sokal and Rohlf [1995]). Means are reported  $\pm 1$  SD. All tests were 2-tailed, and significance was assumed when  $p < 0.05$  although occasionally trends are mentioned when  $0.05 < p < 0.10$ .

## Results

### *Social Structure*

For 50 groups containing both adult males and adult females, accurate counts could be made of their group size, averaging  $7.1 \pm 2.6$  individuals (range 2–13 individuals). On 2 occasions, 2 *P. comata* groups (of 10 and 9 individuals, and 8 and 7 individuals, respectively) remained in close proximity over the course of several hours without any apparent aggressive interaction between them, giving the impression of 2 very large groups. Subsequent observations revealed that they comprised 4 separate groups. None of the groups contained more than 1 adult male and only twice were groups (both comprising 4 individuals) confidently classed as containing only 1 adult male and 1 adult female.

The most frequently recorded group size during the surveys was that of 6 individuals (18% of total). The largest proportion (16%) of individuals in a group was 8, followed by groups of 6 or 9 (Fig. 2). As such, most of the individuals were in groups >6 individuals, and almost half of them in groups of >8 individuals.

Three all-male groups were recorded, and twice a solitary male was observed. Group size of all-male groups averaged  $2.2 \pm 1.3$  individuals (1, 1, 2, 3, and 4 individuals), and these were significantly smaller than 1-male/multifemale groups (Student  $t$  test,  $t = 7.05$ ,  $p = 0.0001$ ). All-male groups, including the 2 solitary males, ranged significantly closer to the forest edge compared to 1-male/multifemale groups (mean distance to edge  $108 \pm 167$  and  $1,007 \pm 1,062$  m, for all-male and 1-male/multifemale groups, respectively;  $t = 5.65$ ,  $p = 0.001$ ), but not at a different altitudinal level (mean altitude  $1,010 \pm 408$  and  $1,118 \pm 538$  m above sea level (a.s.l.), for all-male and 1-male/multifemale groups, respectively;  $t = 0.55$ , ns).

Polyspecific associations between grizzled langurs and other primates were restricted to Javan gibbons, *Hylobates moloch*, or ebony langurs, *Trachypithecus auratus*. The other diurnal primate occurring on Java, the long-tailed macaque *Macaca fascicularis* has a preference for edge and often more disturbed habitats, although in some areas both *M. fascicularis* and *P. comata* occurred sympatrically. Only once did *P. comata* associate with both *H. moloch* and *T. auratus* at the same time. For 6 associations, group sizes of *P. comata* were established confidently. Polyspecific groups often remained stable over the course of several hours and even a number of days. The ratio of the observed number of polyspecific groups versus other groups differed significantly between montane forest ( $>1,500$  m a.s.l.) and lowland to lower montane forest ( $\chi^2 = 5.8$ ,  $df = 1$ ,  $p = 0.02$ ), with more polyspecific groups being observed at higher altitudes. Polyspecific groups showed a tendency to be somewhat smaller than other 1-male/multifemale groups ( $4.8 \pm 2.3$  individuals;  $t = 2.24$ ,  $p = 0.08$ ) and to occur at higher altitudes ( $1,747 \pm 613$  m a.s.l.;  $t = 2.50$ ,  $p = 0.07$ ), but did not range further or closer to the forest edge ( $1,277 \pm 1,378$  m;  $t = 0.55$ , ns).

In terms of composition of bisexual groups, based on results of the survey and data presented in the literature (Table 3), it is clear that over 95% of the groups have only 1 adult male. The number of adult females ranges from 1 to 7 with a mean of  $2.1 \pm 1.4$ , and the infant-adult female ratio is  $0.2 \pm 0.3$ . The overall group size of  $6.1 \pm 2.8$  is somewhat smaller than when combining complete counts with groups with known composition as it is probably easier to confidently identify and sex all individuals in small groups than in large groups.

#### *Correlations between Group Size and Environmental Variables*

There was no apparent variation in group sizes along the latitudinal axis of the island. Annual variation in group sizes was not apparent (1-way ANOVA,  $F_{1,12} = 1.2$ , ns) nor was seasonal variation in group sizes ( $7.1 \pm 2.9$  and  $6.9 \pm 2.2$  individuals for the dry and wet seasons, respectively;  $t = 0.26$ , ns). *P. comata* was recorded only in the wettest parts of Java, and no difference was found in group sizes between areas with hardly any dry season ( $>30$  rainy days during the 4 driest consecutive months) or with a slightly dry season (10–30 rainy days) ( $7.1 \pm 2.7$  and  $6.0 \pm 2.0$  individuals, respectively). Consequently, the effects of season and climate type on group size were not taken into further consideration.

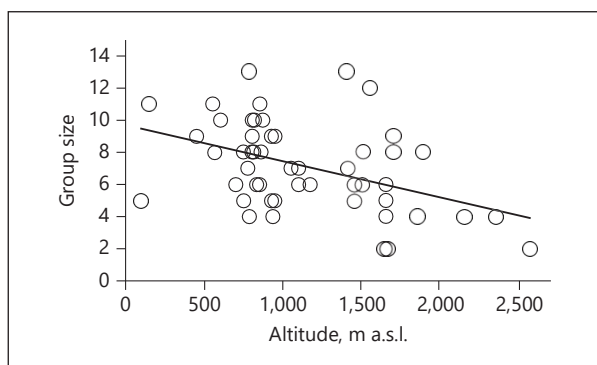
Group size was significantly negatively correlated with altitude ( $F_{15,1} = 4.55$ ,  $R_{adj}^2 = 0.09$ ,  $p = 0.04$ ), and mean group sizes go down roughly by 1 individual with every 600 m rise in elevation (Fig. 3). Mean group size for each of the 12 forest areas was positively correlated with the size of the forest area (log transformed) ( $F_{10,1} = 4.3$ ,  $R_{adj}^2 = 0.23$ ,  $p = 0.07$ ). Group size was positively related to the distance to the forest

**Table 2.** Study areas on the island of Java with altitudinal ranges of the forest and altitudinal ranges of records of grizzled langur (*Presbytis comata*)

Study area and year	Co-ordinates (E-S)	Forest area, km <sup>2</sup>	Complete counts, <i>n</i>	Altitudinal range of, m a.s.l.	
				the forest	the langur groups
1 Ujung Kulon (2000)	105°20', 6°45'	125	1	0–623	50
3 Mt. Aseupan (1997, 2000)	105°57', 6°17'	50	2	100–1,174	100–150
4 Mts. Halimun-Salak (1995–2001)	106°30', 6°40'	550	6	500–2,211	800–1,100
5 Mt. Pancar (1994–2001)	106°54', 6°35'	25	2	650–800	650–800
6 Mts. Gede-Pangrango (1994–2004, 2012–2013)	107°00', 6°45'	180	8	800–3,019	900–1,900
7 Megamendung (1994–2002)	106°55', 6°37'	45	2	900–1,640	900–1,500
8 Cibulau-Telaga Warna (1997–2001, 2013)	106°56', 6°39'	10	1	1,400–1,450	1,400–1,450
9 Telaga Patengan (2000)	107°46', 7°08'	15	6	1,600–1,775	1,650–1,700
12 Mt. Sawal (1995, 2012)	108°16', 7°12'	50	1	700–1,764	900–1,050
14 Mt. Slamet (1994–1995, 1999)	109°15', 7°15'	150	8	700–3,000	700–2,350
15 Mts. Dieng (1994–1995, 1997–2002)	109°49', 7°09'	225	17	300–2,565	400–2,565
17 Mt. Lawu (1994–1995)	111°11', 7°40'	200	1	1,000–3,000	1,900

Study area numbers refer to Figure 1. Complete counts also include counts where the langurs were aged and sexed. Figures in italics refer to the approximate lower or upper altitudinal range of the forest. Additional survey areas within the range of the species, listed from west to east, included Mt. Tangkuban Perahu (1994), Mt. Papandayan (1999, 2012, 2013), Mts. Pembarisan (1994), Mt. Sundoro (1994), Mt. Merbabu (1994), Mt. Merapi (1994, 1995), Mt. Murio (1995) and Mts. Liman-Wilis (1994, 1995). No langurs were seen at any of these sites. a.s.l., above sea level.

**Fig. 3.** Variation in group sizes of 50 bisexual groups of grizzled langur *Presbytis comata* in relation to altitude.



edge (log transformed), however not significantly so ( $F_{46,1} = 2.0, R p = \text{adj}^2 = 0.04, 0.16$ ).

In a simple linear multiple regression model, altitude and distance to the forest edge (log transformed) proved to be the best subset of predictors for the observed variation in group sizes for grizzled langurs. The equation group size =  $4.53 - 0.00167 \text{ altitude} + 1.51 \text{ log distance to the forest edge}$  explained some 17% of the observed variation in group sizes in *P. comata* ( $F_{52,2} = 6.49, p = 0.003$ ).



**Table 3.** Group composition of 66 bisexual groups of grizzled langur (*Presbytis comata*) on Java, grouped by altitude, presenting mean  $\pm$  SD and range

Altitude	Groups	Adult male	Adult female	Subadult	Juvenile	Infant	Total
Lowland and hill (<1,000 m a.s.l.)	14	1.0 $\pm$ 0.0 (1)	3.2 $\pm$ 1.9 (1–7)	1.2 $\pm$ 0.9 (0–3)	1.2 $\pm$ 0.9 (0–2)	0.6 $\pm$ 0.7 (0–2)	7.9 $\pm$ 3.0 (3–13)
Lower montane (1,000–1,500 m a.s.l.)	17	1.1 $\pm$ 0.3 (1–2)	2.1 $\pm$ 1.4 (1–6)	1.2 $\pm$ 1.1 (0–3)	1.4 $\pm$ 0.9 (0–4)	0.5 $\pm$ 0.8 (0–3)	6.3 $\pm$ 2.8 (2–12)
Montane (1,500–2,565 m a.s.l.)	35	1.0 $\pm$ 0.2 (1–2)	1.6 $\pm$ 0.8 (1–5)	1.3 $\pm$ 1.0 (0–4)	1.1 $\pm$ 0.8 (0–3)	0.3 $\pm$ 0.5 (0–2)	5.3 $\pm$ 2.3 (2–11)

Based on data from this study, Istiqamah [2015], Ruhayat [1983, 1991], Nurjaman et al. [2002], Hidayat [2013], Suryana [2010], Sujatnika [1992], and Harjenti [1996]. a.s.l., above sea level.

In terms of composition of bisexual groups, based on results of the survey and data presented in the literature (Table 3) there are clear altitudinal differences. While the number of adult males, subadults, juveniles, and infants does not differ between lowland and hill, lower montane and montane forest, there are clear differences in the total group sizes (1-way ANOVA,  $F_{2,63} = 5.15$ ,  $p = 0.0085$ ) and the number of adult females ( $F_{2,63} = 8.06$ ,  $p = 0.0008$ ); only the differences between groups recorded in the lowland and hill forest and those groups in the montane forest are significant ( $t = 3.28$ ,  $p = 0.0019$ , and  $t = 4.153$ ,  $p = 0.0001$  for group size and number of adult females, respectively) (Table 3). Number of fewer adult females does not translate itself into smaller infant/adult female ratios as these are 0.18 (lowland and hill forest), 0.19 (lower montane forest) and 0.17 (montane forest).

An overview of group sizes in 8 forest areas where *P. comata* has been studied in detail (Table 4) likewise shows a negative relationship between the altitude of the study area and mean group sizes, especially when considering the maximum altitudes at which *P. comata* was observed (data log transformed; minimum elevation: Pearson  $R = -0.595$ ,  $p = 0.091$ ; maximum elevation:  $R = -0.708$ ,  $p = 0.032$ ).

#### *Social Monogamy or Monandry*

Only 2 out of 55 groups could be reliably classed as consisting of 1 adult male/1 adult female with offspring. One of these groups was observed in Telaga Patengan in 2000, where Ruhayat [1983] reported that 4 of his 6 study groups comprised 2 adults plus offspring in 1976–1977. Wedana [1993] reported that 1 of his 4 study groups in Telaga Patengan comprised 1 adult male and 1 adult female, whereas Nurjaman et al. [2002] found 1 of 7 groups in Telaga Patengan to comprise 1 adult male and 1 adult female. Harjenti [1996] studied a population of *P. comata* at elevations between 2,000 and 2,200 m a.s.l. at Brussel on Mt. Patuha, in a straight line 2 km east of Telaga Patengan. She reported that 4 of her 6 study groups comprised a single adult male/single adult female with offspring (2 adult females were present in the remaining 2 groups).

**Table 4.** Examples of areas with mixed lowland rain forest (<500 m a.s.l.), hill forests (500–1,000 m a.s.l.), lower montane forest (1,000–1,500 m a.s.l.), and montane forest (1,500–2,565 m a.s.l.) on Java where grizzled langurs (*Presbytis comata*) have been studied, with information on distribution, abundance, and group sizes

Area	Distribution	Abundance	Mean group sizes, range, and number of sites, <i>n</i>	Population size	References
1 Ujung Kulon	Patchily distributed; possibly disjunct populations on Mt. Honje-Kelejetan and Mt. Payung. Records from sea level to 200 m a.s.l.	Low; approx. 0.6 groups km <sup>-2</sup> in lowland forest; Hoogerwerf, Gurmaya, and Melisch report very few sightings (7, 2 and 0, respectively)	n.a.	Approx. 50 groups?	Hoogerwerf, 1970; Gurmaya et al., 1995; Melisch and Dirgayusa, 1996; Heriyanto and Iskandar, 2004
2 Rawa Danau	Records from 40 to 750 m a.s.l.	Low; approx. 0.4 groups km <sup>-2</sup> in lowland forest	12.6 [5–23], 7	Approx. 10–20 groups	Melisch and Dirgayusa, 1996
13 Mts. Pembarisan-Subang	Records from 250 to 1,250 m a.s.l.	Low; 0.5 groups km <sup>-2</sup> in lowland and hill forest	n.a.	Approx. 300–500 groups; more if extended into Central Java	Supartono et al., 2016
15 Mts. Dieng	Records from 300 to 2,565 m a.s.l.	High: 2.4 groups km <sup>-2</sup> in hill forest	7.1 [2–13], 17	Approx. 400–600 groups; fragmented over altitudinal range	Nijman and van Balen, 1998; Nijman and Nekaris, 2012; this study
11 Mt. Ciremai	Records from 400 to 1,900 m a.s.l.	Low to intermediate: no density estimates available	7.3 [2–18], 27	Approx. 100–200 groups	Wakidi, 2013
4 Mts. Halimun-Salak	Records from 600 to 1,750 m a.s.l.	Low; 0.5 groups km <sup>-2</sup> in hill forest; 0.1 groups km <sup>-2</sup> in lower montane forest; 0.3 groups km <sup>-2</sup> in montane forest	4.8 [2–11], 26	Approx. 200 groups; more if adjacent forest is inhabited	Sugarjito et al., 1997
14 Mt. Slamet	Records from 700 to 2,500 m a.s.l.	Intermediate: 1.5 groups km <sup>-2</sup> in hill forest; 1.7 groups km <sup>-2</sup> in lower montane forest	4.3 [2–14], 18	Approx. 300 groups	Setiawan et al., 2010; this study
10 Kawah Kamojang	Records from 1,350 to 1,600 m a.s.l.	Intermediate: 1.7 groups km <sup>-2</sup> in lower montane forest	7.5 [6–12], 6	Approx. 80–100 groups	Ruhiyat, 1983, 1991
6 Mt. Gede-Pangrango	Records from 900 to 1,900 m a.s.l.	High: 2.4 groups km <sup>-2</sup> in lower montane forest	8.1 [6–13], 13	Approx. 200 groups	Beckwith, 1995; Sugarjito, 1992; this study
10 Mt. Patuha	Records from 1,600 to 2,200 m a.s.l.	High: 3.0–5.8 groups km <sup>-2</sup> in montane forest	5.6 [3–10], 25	Approx. 100–150 groups	Ruhiyat, 1983, 1991; Harjenti, 1996; Nurjaman et al., 2002; this study
16 Mt. Merbabu	Records from 1,900 to 2,550 m a.s.l.	Intermediate: 0.9 groups km <sup>-2</sup> in montane forest	7.2 [4–15], 5	Approx. 20–40 groups?	Syarifah, 2013; Hidayat, 2016
Combined	Sea level to 2,565 m a.s.l.	Lowland: 0.4–0.6 groups km <sup>-2</sup> Hill: 0.5–2.4 groups km <sup>-2</sup> Lower montane: 0.1–2.4 groups km <sup>-2</sup> Montane: 0.3–5.8 groups km <sup>-2</sup>	7.2 [2–23], 12	Approx. 1,760–2,360 groups	

Sites are ordered by lowest altitude of encounters with langurs. When only encounter rates are reported, densities are estimated using an effective strip width of 50 m. Population size estimates are based on densities, the amount of available forest and the distribution of langurs within the forest. n.a., not available; a.s.l., above sea level.

## Discussion

### *Distribution and Social Organization*

*P. comata* is distributed in the last remaining forest areas of Java, where it can be found as far east as Mt. Merbabu and Mt. Lawu on the border with East Java. Large-scale deforestation in especially the lowlands and hill zones means that many populations are confined to montane areas, and here the species can be found at high altitudes up to 2,565 m a.s.l. Comparisons with the 15 other species of *Presbytis* langurs (with the exception of the monogamous *P. potenziani* and the possibly monandrous *P. frontata*) shows that throughout most of its range *P. comata* is a rather typical representative of the genus [reviewed in Newton and Dunbar, 1994; Bennett and Davies, 1994; Yeager and Kirkpatrick, 1998; Yeager and Kool, 2000; Sterck, 2012; Zinner et al., 2013]. In terms of the most common social unit (1 male/multiple females with offspring), male emigration (as suggested by the presence of solitary males, all-male groups), group size (means of 6–7 individuals) and habitat use (undisturbed lowland forest preferred over degraded forests and plantations [Nijman, 1997b, 2010]), the species shows no anomalies. Groups with 2 adult males/multiple females have been recorded, but very infrequently, while 1-male/1-female groups do occur in certain areas.

All-male groups seemed to have at least partially different ranging patterns and possibly show different habitat use than 1-male/multifemale groups, as they were significantly more often found close to the forest edge. Differential habitat use or ranging patterns of all-male and bisexual groups are scarcely documented but have been reported for *P. thomasi* [Steenbeek, 1999] and the pale-thighed langur *P. siamensis* [Bennett, 1983].

*P. comata* infrequently forms polyspecific associations with other langurs and gibbons. Polyspecific associations between *Presbytis* and other langurs (*Presbytis*, *Trachypithecus*, *Nasalis*) have been reported [e.g., Bartels, 1937; Medway, 1970; Curtin, 1980; Ruhiyat, 1983; Wakidi, 2013; Rowe and Myers, 2017] although in South-East Asian rain forest polyspecific associations between primates are far less common than in African or Neotropical forests [Chapman and Chapman, 2000; Heymann and Buchanan-Smith, 2000; Fam and Nijman, 2011]. It is suggested that polyspecific associations are formed under predation pressure [e.g., Struhsaker, 1981, 2000; Noë and Bshary, 1997]. Differences between Africa and the Neotropics on the one hand and Asia on the other have most commonly been explained by differences in predation pressure, in particular the apparent absence of specialized primate-targeting raptors in Asia [Hart, 2007; Fam and Nijman, 2011].

Compared to other *Presbytis* langurs studied to date, *P. comata* does occur over a large altitudinal range with resident populations occurring in upper montane forests >2,000 m a.s.l. Polyspecific associations were mostly found at high altitudes, and *P. comata* groups that were part of such polyspecific associations showed a tendency to be smaller than other groups. Struhsaker [1981] noted a relation between the formation of polyspecific associations and group size, with species with smaller group sizes being more often the initiator of the formation. The relatively high occurrence of polyspecific associations in *P. comata* at high altitudes may be a response to overcome the negative effects of small group sizes that are imposed by the low productivity of the environment. In order to test this notion, however, more quantitative data are needed about predator pressure, densities and productivity of the forest at the different altitudinal levels.

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### *Altitudinal Variation in Ecology, Group Size, and Composition*

*P. comata* has been considered to be essentially confined to lowland and hill forest below 1,250 m a.s.l. [e.g., Hoogerwerf, 1970; Medway, 1970; Whitten et al. 1996], or alternatively to a small narrow band between 1,200 and 1,800 m a.s.l. [Supriatna et al. 1994; Rowe, 1996], but in fact it occurs from sea level to >2,500 m a.s.l. (Tables 2–4). In some areas *P. comata* has been repeatedly recorded at altitudes >2,000 m a.s.l. [Harjenti, 1996; Nijman and van Balen, 1998; Syarifah, 2013; Hidayat, 2016; this study], amidst dwarfed forests, suggesting resident populations. Invariably these groups consisted of only a few individuals. Given the lower primary production of montane forests compared to forests at lower elevations with a different species composition [Whitten et al., 1996] population densities of primates on Java are lower at higher altitudes [Sugarjito et al. 1997; Nijman, 2015]. The difference in structure and species composition between lowland and hill forest and montane forest reflects itself in pronounced differences in the diet of *P. comata* [Kavana et al., 2015; Yang et al., 2016]. Ruhayat [1983] found the species to be largely folivorous at altitudes between 1,400 and 1,650 m a.s.l., with 65.2% of the diet comprising leaves and flowers (59.1% young leaves; 5.6% mature leaves, 7% flowers) and only 14.2% comprising fruits and seeds (13.5% fruit, 0.7% seeds). This is similar to that reported by Sujatnika [1992] from similar altitudes (1,250–1,550 m a.s.l.) on Mt. Gede-Pangrango, i.e., 65.0% young leaves, 5.0% mature leaves, 17.0% flowers, 6.4% fruits, and 2.3% seeds. At lower elevations the species is more frugivorous. Sugiarto [2006] studied the species at 700 m a.s.l. on Mt. Pangrango where 38.2% of the diet comprised fruits and seeds and 59.6% leaves. Suryana [2010] studied the species at 500–600 m a.s.l. in Mts. Dieng and found it to feed largely on fruits and seeds (i.e., 24.9% seeds, 17.2% fruits and seeds, 8.9% fruits) and to a lesser extent on leaves and flowers (i.e., 35.8% young leaves, 4.0% mature leaves, and 1.6% flowers). A diet comprised largely of fruits and seeds is very much in line to that which has been reported for the majority of other *Presbytis* species [e.g., Bennett and Davies, 1994].

The montane environment may impose a selective pressure towards not only smaller group sizes and a different diet, but also a different social system, with ultimately monandry or monogamy as a more favourable evolutionary strategy. The reduction in group sizes along the altitudinal gradient was driven largely by a reduction in the number of adult females that were present in higher-altitude groups, and not by a difference in the number of adult males, subadults, or infants. In non-territorial groups it is probably the dispersion, quality, and size of the food patches within the group's range, rather than the size of the home range, that determine the ability of males to maintain exclusive access to females. Male *P. comata* are unlikely to defend food sources so there is little advantage for females to associate with more than 1 adult male. In poor-quality habitat, relative to the langur's specific feeding needs, high group cohesion, especially for larger groups, can only be maintained by ranging further, at a greater speed, whilst feeding on fewer and lower-quality food patches [Beckwith, 1995]. The body size of *P. comata*, its locomotor behaviour and arboreal needs, and its digestive strategy limit these options, but reducing group sizes may allow it to persist in low-quality habitats.

Both males and females disperse in *Presbytis* [Sterck et al., 2005], and new group formation can be achieved by a number of females splitting from the main group while being joined by an outside male [Davies, 1987]. Females can also join neighbouring groups, with females from large groups often joining smaller groups [Sterck, 1997].

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Steenbeek and van Schaik [2001] found that in *P. thomasi* the upper limit to group size was not set by feeding competition. Instead, they suggested that female reproductive success was maximized in small to mid-sized groups because larger groups show a clear trend to experience a higher risk of take-over. Females can redistribute themselves either by forming new groups or by joining nearby groups during male tenure change, and by doing so adult females can keep the group small [Steenbeek and van Schaik, 2001]. While there are no altitudinal differences in reproductive success for adult females, it appears that in *P. comata* selective pressures differ with altitude, and possibly females disperse sooner or more frequently forming new, small, groups at higher elevations.

#### *Evidence for Monandry*

If monandry or social monogamy is expected in *P. comata*, it is most likely at high altitudes. Small group sizes however do not necessarily imply a monogamous mating pattern. In the present study, several groups were observed to show considerable spatial overlap indicating the potential for intergroup copulations. It has been argued that monogamy has to be defined as a prolonged association (>1 breeding cycle) and essentially exclusive mating relationship between 1 male and 1 female [Fuentes, 2000]; these data are lacking for *P. comata*.

In the present survey 2 out of 55 groups could be reliably classed as 1-male/1-female with offspring, but no data were obtained on whether these small groups persist over long periods of time. Data from the forests of Telaga Patengan and adjacent Brussel collected intermittently between 1976 and 2002, however, suggest that in the forest of Mt. Patuha 1-male/1-female groups are consistently present alongside 1-male/multifemale groups. The five 1-male/multifemale groups observed in Telaga Patengan averaged 6 individuals, and this is only slightly below the average for Java as a whole (Table 3). Ruhiyat [1983] drew attention to the unusual group composition, the high population density, the unusual high overlap between groups, and the frequent splitting of 1 of the larger groups (10 individuals including 2 adult males) into 2 smaller groups (each containing 1 adult male). He attributed this to the recent isolation and strong reduction of the forest area around Telaga Patengan (due to an enlargement of the surrounding tea plantation and due to logging) and suggested that at least 2 of the groups had only very recently moved into his study area [Ruhiyat, 1991, p. 165]. The atypical situation at Telaga Patengan was the reason to move his study to another, less disturbed site [Ruhiyat, 1983, 1991]. Group sizes in *P. comata* are positively correlated with forest area and distance to the forest edge and are furthermore negatively related with altitude. Smaller than average group sizes are hence expected in small or highly fragmented high-altitude forest areas, of which Telaga Patengan (1,650 m a.s.l., 10–15 km<sup>2</sup>) is a prime example.

#### **Conclusions**

For 3 decades after Ruhiyat [1983] had published the results of his fieldwork, his findings were often the only ones used for *P. comata* in comparative studies [e.g., van Schaik and Hörstermann, 1994; Bennett and Davies, 1994; Wright and Willis, 2012; Tsuji et al., 2013]. Other studies that were published on *P. comata* in mainstream scientific journals over this period that contained primary data dealt with distribution,

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conservation, or taxonomy [Weitzel and Groves, 1985; Melish and Dirgayusa, 1996; Nijman, 1997a, b; Nijman and van Balen, 1998; Meyer et al., 2011; Supartono et al., 2016]; the few ecological studies that were conducted either appeared in Indonesian journals, internal reports or remained hidden in unpublished theses [Sujatnika, 1992; Wedana, 1993; Nurdiana, 1997; Sugarjito et al., 1997; Nurjaman et al., 2002; Heriyanto and Iskandar, 2004; Suryana, 2010; Sawitri et al., 2010; Syarifah, 2013; Hidayat, 2016]. As such, the populations of *P. comata* that were present in Kawah Kamojang and Telaga Patengan in the 1970s have become the standard for the species, ignoring (perhaps unintentionally) the socioecological intraspecific variation that is present. The present study showed that the variation in group sizes and group composition in *P. comata* can, at least in part, be explained by environmental variables such as altitude and forest characteristics. Within primates, there does not seem to be a single prime correlate of social monogamy. Instead, social monogamy may result from an array of selective pressures that act alone or in combination, some more important, some less important in a given environment at a given time [cf. Thalmann, 2001]. The role of environmental factors (climate, productivity, disturbance) in shaping the social system within species seems to be rarely quantified, and this may be a promising avenue along which to proceed with further research.

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There is no conflict of interest to declare.

## References

- Anschel S, Talmage-Riggs G (1977). Social organization of captive monandrous squirrel monkey groups (*Saimiri sciureus*). *Folia Primatologica* 28: 203–215.
- Bartels M (1937). Zur Kenntnis der Verbreitung und der Lebensweise javanischer Säugetiere. *Treubia* 16: 149–164.
- Beckwith RS (1995). *The Ecology and Behaviour of the Javan Black Langur, in a Lower Montane Rain Forest, West Java*. PhD thesis, University of Cambridge.
- Bennett EL (1983). *The Banded Langur: Ecology of a Colobine in a West Malaysian Rainforest*. PhD thesis, University of Cambridge.
- Bennett EL, Davies AG (1994). The ecology of Asian colobines. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Davies AG, Oates JF, eds.), pp 129–171. Cambridge, Cambridge University Press.
- BPS (2017). *Kepadatan penduduk menurut provinsi 2000–2015*. Badan Pusat Statistik Indonesia. [www.bps.go.id](http://www.bps.go.id).
- Brandon-Jones D (1995). *Presbytis fredericae* (Sody, 1930), an endangered Colobine species endemic to Central Java, Indonesia. *Primate Conservation* 16: 68–70.
- Chapman CA, Chapman LJ (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology* 21: 565–585.
- Curtin SH (1980). Dusky and banded leaf monkeys. In *Malayan Forest Primates: Ten Years' Study in Tropical Rainforest* (Chivers DJ, ed.), pp 107–145. New York, Plenum Press.
- D'Agostino J, Spehar SN, Delgado R (2016). The behavioural contexts of red langur (*Presbytis rubicunda*) loud calls in the Wehea Forest, East Kalimantan, Indonesia. *Folia Primatologica* 87: 1–10.
- Davies AG, Oates JF (1994). *Colobine Monkeys: Their Ecology, Behavior and Evolution*. Cambridge, Cambridge University Press.
- Davies G (1987). Adult male replacement and group formation in *Presbytis rubicunda*. *Folia Primatologica* 49: 111–114.
- Dixon AF (1995). Sexual selection and ejaculatory frequencies in primates. *Folia Primatologica* 64: 146–152.
- Fam SD, Nijman V (2011). *Spizaetus* hawk-eagles as predators of arboreal colobines. *Primates* 52: 105–110.
- Fuentes A (2000). Hylobatid communities: changing views on pair bonding and social organization in hominoids. *Yearbook of Physical Anthropology* 43: 33–60.
- Groves CP (2001). *Primate Taxonomy*. Washington, Smithsonian Institution Press.
- Gurmaya KJ, Adiputra IMW, Saryatiman AB, Danardono SM, Sibuea TT (1995). *Primate Survey, Population and Ecology: Gunung Honje Range Ujung Kulon National Park. Ujung Kulon National Park Project Phase II, 1993–1995*. Jakarta, Department Kehutanan and New Zealand Ministry of Foreign Affairs and Trade.
- Hart D (2007). Predation on primates: a biogeographical analysis. In *Primate Anti-Predator Strategies* (Gursky SL, Nekaris KAI, eds.), pp 27–59. New York, Springer.
- Harjenti TD (1996). *Perilaku Makan dan Jenis Makanan Surili (Presbytis comata Desmarest 1922) di Hutannya, Gunung Patuha, Cidewey, Jawa Barat*. BSc thesis, Universitas Padjadjaran, Bandung.
- Heriyanto NM, Iskandar S (2004). Status populasi dan habitat surili *Presbytis comata* Desmarest di kompleks hutan Kelajeten – Karangranjang, Taman Nasional Ujung Kulon. *Jurnal Penelitian Hutan dan Konservasi* 1: 89–98.
- Heymann EW, Buchanan-Smith HM (2000). The behavioral ecology of mixed-species troops of callitrichine primates. *Biological Reviews* 75: 169–190.
- Hidayat R (2013). *Pendugaan Parameter Demografi dan Pola Penggunaan Ruang Surili (Presbytis comata) di Taman Nasional Gunung Ciremai*. BSc thesis, Institut Pertanian Bogor.
- Hidayat S (2016). *Pengelolaan Taman Nasional Gunung Merbabu Sebagai Konservasi Rekrakan (Presbytis fredericae)*. MSc thesis, Universitas Sebelas Maret, Surakarta.
- Hoogerwerf A (1970). *Ujung Kulon, the Land of the Last Javan Rhinoceros*. Leiden, Brill.
- Istiqumah DR (2015). *Karakteristik Habitat Populasi dan Penyebaran Rekrakan (Presbytis fredericae, Sody 1930) di Resort Semuncar, Taman Nasional Gunung Merbabu*. BSc thesis, Institut Pertanian Bogor.
- Kavana TS, Erinjery JJ, Singh M (2015). Folivory as a constraint on social behaviour of langurs in south India. *Folia Primatologica* 86: 420–431.
- Lammertink M, Nijman V, Setiawati U (2003). Population size, Red List status and conservation of the Natuna leaf monkey *Presbytis natunae* endemic to the island of Bunguran, Indonesia. *Oryx* 37: 472–479.
- Leutenegger W (1982). Scaling of sexual dimorphism in body weight and canine size in primates. *Folia Primatologica* 37: 163–176.
- Leutenegger W, Lubach G (1987). Sexual dimorphism, mating system, and effect of phylogeny in De Brazza's monkey (*Cercopithecus neglectus*). *American Journal of Primatology* 13: 171–179.
- Lott DT (1991). *Intraspecific Variation in the Social System of Wild Vertebrates*. Cambridge, Cambridge University Press.
- Lukas D, Clutton-Brock TH (2013). The evolution of social monogamy in mammals. *Science* 341: 526–530.
- Medway L (1970). The monkeys of Sundaland, ecology and systematics of the cercopithecids of a humid equatorial environment. In *Old World Monkeys, Evolution, Systematics and Behavior* (Napier JR, Napier PH, eds.), pp 513–553. New York, Academic Press.
- Melisch R, Dirgayusa IWA (1996). Notes on the grizzled leaf monkey (*Presbytis comata*) from two nature reserves in West Java, Indonesia. *Asian Primates* 6: 5–11.
- Meyer D, Rinaldi ID, Ramee H, Perwitasari-Farajallah D, Hodges JK, Roos C (2011). Mitochondrial phylogeny of leaf monkeys (genus *Presbytis*, Eschscholtz, 1821) with implications for taxonomy and conservation. *Molecular Phylogenetics and Evolution* 59: 311–319.

- Newton PN, Dunbar RIM (1994). Colobine monkey society. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Davies AG, Oates JF, eds.), pp 311–346. Cambridge, Cambridge University Press.
- Nijman V (1997a). Geographical variation in pelage characteristics in *Presbytis comata* (Desmarest, 1822) (Mammalia: Primates: Cercopithecidae). *Zeitschrift für Säugetierkunde* 62: 257–264.
- Nijman V (1997b). On the occurrence and distribution of *Presbytis comata* (Desmarest 1822) (Mammalia: Primates: Cercopithecidae) on Java, Indonesia. *Contributions to Zoology* 66: 247–256.
- Nijman V (2010). Ecology and conservation of the Hose's langur group (Colobinae: *Presbytis hosei*, *P. canicrus*, *P. sabana*): a review. In *Behavior, Ecology and Conservation of Indonesian Primates* (Gursky S, Supriatna J, eds.), pp 269–284. New York, Springer.
- Nijman V (2013). One hundred years of solitude: effects of long-term forest fragmentation on the primate community of Java, Indonesia. In *Primates in Fragments: Complexity and Resilience* (Marsh LK, Chapman CA, eds.), pp 33–45. New York, Springer.
- Nijman V (2015). Distribution and ecology of the most tropical of the high-elevation montane colobines: the ebony langur on Java. In *High Altitude Primates* (Grow NB, Gursky-Doyen S, Krzton A, eds.), pp 115–132. New York, Springer.
- Nijman V, Nekaris KAI (2012). Loud calls, startle behaviour, social organisation and predator avoidance in arboreal langurs (Cercopithecidae: *Presbytis*). *Folia Primatologica* 83: 274–287.
- Nijman V, Richardson M (2008). *Presbytis comata*. The IUCN Red List of Threatened Species 2008: e.T18125A7664645. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T18125A7664645.en>.
- Nijman V, van Balen S (1998). A faunal survey of the Dieng Mountains, Central Java, Indonesia: status and distribution of endemic primate taxa. *Oryx* 32: 145–156.
- Nijman V, Spaan D, Rode-Margono EJ, Nekaris KAI (2015). Changes in the primate trade in Indonesian wildlife markets over a 25-year period: fewer apes and langurs, more macaques and slow lorises. *American Journal of Primatology* DOI: 10.1002/ajp.22517.
- Noë R, Bshary R (1997). The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London, Series B* 264: 253–259.
- Nurdiana (1997). *Pola Aktivitas Harian dan Penggunaan Strata Vegetasi pada Suruli (Presbytis comata comata Desmarest, 1822) di Cikaniki, Taman Nasional Gunung Halimun, Jawa Barat*. BSc thesis, Universitas Padjadjaran, Bandung.
- Nurjaman N, Bismark M, Iskandar S (2002). Status populasi dan kondisi habitat suruli (*Presbytis comata*) di cagar alam Situ Patengan, Jawa Barat. *Berita Biologi* 6: 455–459.
- Opie C, Atkinson QD, Dunbar RI, Shultz S (2013). Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences* 110: 13328–13332.
- RePPPProT (1990). *The Land Resources of Indonesia: A National Overview from the Regional and Physical Planning Program for Transmigration*. London and Jakarta, Land Resources Department, National Institute Overseas Development Administration and Direktorat Bina Program, Direktorat Penyediaan Pemukiman, Department Transmigrasi.
- Roldan ERS, Gomendio M (1995). Sperm length and sperm competition in primates: a rebuttal of criticism. *Folia Primatologica* 64: 225–230.
- Rowe N (1996). *The Pictorial Guide to the Living Primates*. East Hampton, Pogonias Press.
- Rowe N, Myers M (2017). *All the World Primates*. East Hampton, Pogonias Press.
- Ruhayat Y (1983). Socio-ecological study of *Presbytis aygula* in West Java. *Primates* 24: 344–359.
- Ruhayat Y (1991). Observations of *Presbytis aygula* in two localities of Java. *Comparative Primatological Monographs* 3: 149–191.
- Sawitri R, Mukhtar AS, Iskandar S (2010). Status konservasi mamalia dan burung di Taman Nasional Merbabu. *Jurnal Penelitian Hutan dan Konservasi Alam* 7: 227–239.
- Setiawan A, Wibisono Y, Nugroho TS, Agustin IY, Imron MA, Pudyatmoko S (2010). Javan suruli: a survey population and distribution in Mt. Slamet, Central Java, Indonesia. *Jurnal Primatologi Indonesia* 7: 51–54.
- Smith RJ, Jungers WL (1997). Body mass in comparative primatology. *Journal of Human Evolution* 32: 523–559.
- Sokal RR, Rohlf FJ (1995). *The Principles and Practice of Statistics in Biological Research*. New York, Freeman & Co.
- Steenbeek R (1999). Tenure related changes in wild Thomas's langurs. I. Between group interactions. *Behaviour* 136: 595–625.
- Steenbeek R, Assink P (1998). Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). *Folia Primatologica* 69: 77–80.
- Steenbeek R, van Schaik CP (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology* 49: 100–110.
- Sterck EH (1997). Determinants of female dispersal in Thomas langurs. *American Journal of Primatology* 42: 179–198.
- Sterck EHM (2012). The behavioural ecology of colobine monkeys. In *The Evolution of Primate Societies* (Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JA, eds.), pp 65–90. Chicago, University of Chicago Press.
- Sterck EHM, Willems EP, van Hooft JARAM, Wich SA (2005). Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). *Behaviour* 142: 845–868.
- Struhsaker TT (1981). Polyspecific associations among tropical rain-forest primates. *Zeitschrift für Tierpsychologie* 57: 268–304.
- Struhsaker TT (2000). The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In *Old World Monkeys* (Whitehead PF, Jolly CJ, eds.), pp 393–430. Cambridge, Cambridge University Press.



- Sugarjito J, Sinaga MH, Yoneda M (1997). Survey of the distribution and density of primates in Gn Hali- mun National Park, West Java, Indonesia. In *The Inventory of National Resources in Gunung Hali- mun National Park* (Simbolon H, ed.), vol II, pp 56–62. Bogor, LIPI, JICA, PHPA.
- Sugiarto U (2006). *Studi Populasi dan Penggunaan Habitat Surili (Presbytis comata Linnaeus, 1758) di Hutan Bodogol, Resort Bodogol, Taman Nasional Gunung Gede Pangrango*. BSc thesis, Universitas Nusa Bangsa, Bogor.
- Sujatnika (1992). *Studi Habitat Surili (Presbytis aygula Linnaeus, 1758) dan Pola Penggunaannya di Taman Nasional Gunung Gede-Pangrango dan Kawasan Hutan Haurbentes-Jasinga*. BSc thesis, Institut Pertanian Bogor.
- Supartono T, Prasetyo LB, Hikmat A, Kartono AP (2016). Spatial distribution and habitat use of Javan langur (*Presbytis comata*): case study in District of Kuningan. *Procedia Environmental Sciences* 33: 340–353.
- Supriatna J, Tilson R, Gurmaya KJ, Manansang J, Wardojo W, Sriyanto A, Teare A, Castle K, Seal U (1994). *Javan Gibbon and Javan Langur, Population and Habitat Viability Analysis Report*. Cisarua, Captive Breeding Specialist Group Species Survival Commission of the IUCN and Taman Safari Indonesia.
- Suryana D (2010). *Studi Perilaku Makan dan Palatabilitas Rekrekan (Presbytis fredericae Sody, 1930) di Kawasan Hutan dan Perkebunan Karet Desa Gutomo Kabupaten Pekalongan Provinsi Jawa Tengah*. BSc thesis, Institut Pertanian Bogor.
- Syarifah (2013). *Seleksi Habitat oleh Rekrakan (Presbytis fredericae Sody, 1930) di Taman Nasional Gunung Merbabu*. BSc thesis, Universitas Gajah Mada, Yogyakarta.
- Tenaza RR, Fuentes A (1995). Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. *International Journal of Primatology* 16: 295–310.
- Thalmann U (2001). Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *International Journal of Primatology* 22: 287–324.
- Tilson RL, Tenaza RR (1976). Monogamy and duetting in an Old World monkey. *Nature* 263: 320–321. Trevithick A (1997). On a panhuman preference for monandry: is polyandry an exception? *Journal of Comparative Family Studies* 28: 154–181.
- Tsuji Y, Hanya G, Grueter CC (2013). Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates* 54: 201–215.
- van Balen S, Nijman V, Sözer R (2001). Conservation of the endemic Javan hawk-eagle *Spizaetus bartelsi* Stresemann, 1924 (Aves: Falconiformes): density, age-structure and population numbers. *Contributions to Zoology* 70: 161–173.
- van Schaik CP, Hörstermann M (1994). Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology and Sociobiology* 35: 261–272.
- Van Steenis CGGJ (1972). *The Mountain Flora of Java*. Leiden, Brill.
- Vun VF, Mahani MC, Lakim M, Ampeng A, Md-Zain BM (2011). Phylogenetic relationships of leaf monkeys (*Presbytis*; Colobinae) based on cytochrome b and 12S rRNA genes. *Genetic and Molecular Research* 10: 368–381.
- Wakidi (2013). *Studi Kohabitasi Penggunaan Ruang Lutung dengan Surili di Taman Nasional Gunung Ciremai Provinsi Jawa Barat*. BSc thesis. Bogor, Intitut Pertanian Bogor.
- Watanabe K (1981). Variations in group composition and population density of the two sympatric Men-tawaian leaf-monkeys. *Primates* 22: 145–160.
- Wedana IM (1993). *Perilaku Makan Pada Surili (Presbytis comata comata Desmarest 1822) di Cagar Alam Situ Patengan Jawa Barat*. BSc thesis, Universitas Padjadjaran, Bandung.
- Weitzel V, Groves CP (1985). The nomenclature and taxonomy of the colobine monkeys of Java. *International Journal of Primatology* 6: 399–409.
- Whitten T, Soeriaatmadja RE, Afiff SA (1996). *The Ecology of Java and Bali*. Singapore, Periplus.
- Willis MS, Swindler DR (2004). Molar size and shape variations among Asian colobines. *American Journal of Physical Anthropology* 125: 51–60.
- Wright BW, Willis MS (2012). Relationships between the diet and dentition of Asian leaf monkeys. *American Journal of Physical Anthropology* 148: 262–275.
- Yang B, Zhang P, Garber PA, Hedley R, Li B (2016). Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) consume cicadas in the Qinling Mountains, China. *Folia Primatologica* 87: 11–16.
- Yeager CP, Kool KM (2000). The behavioural ecology of Asian colobines. In *Old World Monkeys* (White-head PF, Jolly CJ, eds.), pp 496–521. Cambridge, Cambridge University Press.
- Yeager CP, Kirkpatrick RC (1998). Asian colobine social structure: ecological and evolutionary constraints. *Primates* 39: 147–155.
- Zinner D, Fickenscher G, Anandam M, Bennett EL, Davenport TRB, Davies N, Engelhardt A, Eudey AA, Gadsby EL, Groves CP, Healy A, Karanth KP, Molur S, Nadler T, Richardson M, Riley EP, Sheeran LK, Ting N, Wallis J, Waters S, Whittaker D, Roos C (2013). Old World monkeys (Cercopithecidae) In *Handbook of the Mammals of the World* (Mittermeier RA, Rylands A, Wilson DE, eds.), vol 3: Primates, pp 628–753. Barcelona, Lynx.