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Distribution and Ecology of the Most Tropical of the High-Elevation Montane Colobines: The Ebony Langur on Java

Vincent Nijman

Introduction

Colobines are distributed over a wide range of habitats, and the Asian taxa occupy a distinctly larger range of habitats than their African counterparts (Kirkpatrick 2011; Fashing 2011). These habitats include various hill and mountain ranges. In Africa, it appears that only the Ethiopian highlands support permanent populations of a colobine, i.e. black-and-white colobus *Colobus guerza*, occurring up to 3,300 m.a.s.l. (Dunbar and Dunbar 1974). With respect to the occurrence of high-elevation colobines two large mountain areas stand out: (1) the mountains of south and central China where various species of snub-nosed monkey of the genus *Rhinopithecus* occur, and (2) the Himalayas, where in addition to snub-nosed monkeys several langurs occur. In the Northeastern parts of the Himalayas, the Burmese snub-nosed monkey *R. strykeri* is confined to a small high-altitude region (Geissmann et al. 2010), in the Southeastern parts several langurs of the genus *Trachypithecus* occur and throughout the Himalayas various species of hanuman langur of the genus *Semnopithecus* are found. Most of these species range from lowland into the montane areas, typically to about 2,500–3,000 m.a.s.l.[asl] (Table 1), with the hanuman langurs and the black snub-nosed monkey occurring, at least seasonally, above 4,000 m.a.s.l.

As can be seen in Table 1, a number of these high altitude colobines appear to be confined to montane regions with no extant populations occurring in the lowlands. This is especially true for the high-elevation montane hanuman langurs and the Chinese and Burmese snub-nosed monkeys. While the Himalayan hanuman langurs may indeed have evolved to persist in these montane regions (with several of their congeners being distributed allopatrically in the low-lying parts of the Indian Subcontinent), for the snub-nosed monkeys their exclusive montane

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Table 1 Colobines living in montane areas above 2,500 m.a.s.l., showing that all but one species occur in Asia with only four species (still) ranging from sealevel to the high mountains

Species	Altitudinal range	Montane range	Reference
Black snub-nosed monkey *Rhinopithecus bieti*	3,000–4,700	China	Kirkpatrick and Grueter (2010)
Grey snub-nosed monkey *R. brelechi*	1,400–2,300	China	Kirkpatrick and Grueter (2010)
Golden snub-nosed monkey *R. roxellana*	1,400–2,800	China	Kirkpatrick and Grueter (2010)
Myanmar snub-nosed monkey *R. strykeri*	1,700–3,200	Himalayas	Geissmann et al. (2010)
Gee's golden langur *Trachypithecus geei*	0–3,000	Himalayas	Choudhury (2008)
Capped langur *T. pileatus*	0–3,000	Himalayas	Choudhury (2008)
Kashmir hanuman langur *Semnopithecus ajax*	2,200–4,000	Himalayas	Minhas et al. (2010)
Nepal hanuman langur *S. schistaceus*	1,500–4,000	Himalayas	Sayers and Norconk (2008)
Ebony langur *T. auratus*	0–3,500	Java	Nijman (2000)
Black-and-white colobus *Colobus guereza*	0–3,300	Ethiopian highlands	Dunbar and Dunbar (1974)

distribution is almost certainly an artefact of the extinction of their populations at lower elevations. Li et al. (2002) report on the distribution of snub-nosed monkeys in China showing that in historic times these species indeed did occur at lower elevations down to 300 m.a.s.l. The langurs of the genus *Trachypithecus* and indeed the black-and-white colobus can still be found from sealevel up to the highest mountains in their respective ranges.

It is worthwhile noting that most of these high-elevation colobines live on the northernmost parts of their generic ranges, in areas that experience the largest amount of seasonal climatic changes. While few populations have been studied in great detail, for a fair number of these colobines it has been reported that they show a considerable amount of seasonal altitudinal migration. During the coldest parts of the years groups and populations migrate to lower elevations, only to take advantage of the milder conditions in summer allowing them to move higher up the mountains (Bishop 1979; Lui et al. 2004; Kirkpatrick and Grueter 2010; Geissmann et al. 2010; Niu et al. 2010). While these species occur at higher latitudes, typically north of the Tropic of Cancer thus outside the tropics, the ebony langur *Trachypithecus auratus* of the Indonesian islands of Java, Bali and Lombok, is the most tropical of all high-altitude colobines living very close to the equator.[1]

[1] The other colobine endemic to Java, the grizzled langur *Presbytis comata*, has been recorded in Montane Zone such as on Mt Pangrango (up to 2,600 m.a.s.l.), Mt Slamet (up to 2,350 m.a.s.l.) and Mt Prahu (up to 2,565 m.a.s.l.). Overall, however, the species appears to be much more confined to the forest of the lowland to Submontane Zones (Nijman 1997).

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Here I provide an overview of the distribution and ecology of the ebony langur, focussing on the island of Java, emphasising their occurrence in high-altitude areas. Distinctly different from other regions where high-elevation colobines occur, I first provide a physical description of the island of Java and its montane environment. I document the distribution of ebony langurs in these mountains, emphasising their presence in the higher regions, note the occurrence of frost on these regions, and compare them to adjacent lowland areas. Finally, I present the results of surveys conducted on the island showing that there is a clear relationship between rainfall, elevation and group sizes and densities of ebony langurs.

Methods

Study Area

The island of Java, Indonesia's political and industrial centre, is one of the most densely populated areas in the world. The very fertile soils which lend themselves to terracing for irrigated rice, sustain about 121 million inhabitants, at an average population density of 914 people km^{-2} (data from 2000: BPS 2004). Java is largely deforested and most of the remaining forest fragments cover (parts of) the numerous volcanoes on the island. The remainder is essentially a mosaic of rice fields, cities and villages. Java has a long history of cultivation and deforestation that already started ca. 1,000 AD, but really took off in 1830 when the Dutch colonial Government imposed the so-called 'cultuurstelsel'. To support this agro-economic system, farmers were forced to grow export crops on communal grounds, which was often forest (Whitten et al. 1996). By the end of the nineteenth century the natural forest was severely fragmented, and at the beginning of the last century the remaining forest showed a fragmentation pattern very similar to that seen today (Fig. 1). At present, as little as 2 % of the original forest in the fertile lowlands remains; in the mountains, especially at higher elevations, about half of the original forest remains standing (Smiet 1992). Permanent human occupation in AQ1 the mountains is less dense than in the lowland, and in most areas few if any villages are situated outside the submontane level above 1,600 m.a.s.l.; the highest villages in Java are situated between 2,000 and 2,100 m.a.s.l. on the Dieng plateau (number 19 in Fig. 1) and Mt Semeru [30]. AQ2

It is true to say that the physical landscape of Java is dominated by its mountains (Stehn 1933), many of which are of volcanic origin. Most mountains are situated along the longitudinal axis of the island, with the mountains in the west forming a large cluster less interrupted by the low-lying plains than the more separated mountains in the east. In the province of West Java there are 12 peaks above 2,000 m.a.s.l. with the highest being Mts Gede-Pangrango [3,019 m.a.s.l. (number 6 in Fig. 1)] and Mt Ciremai (3,078 m.a.s.l. [12]). In Central Java there are 7 such peaks, the highest being Mt Slamet (3,432 m.a.s.l. [17]), and in East Java there are

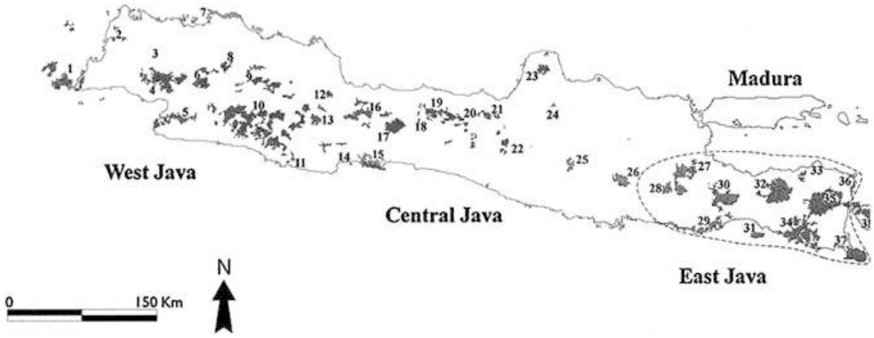

Fig. 1 Geographic distribution of ebony langur *Trachypithecus auratus* on Java, Indonesia, indicated in *grey* (after Nijman 2000). Montane populations are found in (**4**) Mts Halimun-Salak, (**6**) Mt Gede Pangrango, (**9**) Mt Tangkuban Perahu, (**10**) Mt Papandayan, (**12**) Mt Ceremai, (**17**) Mt Slamet, (**19**) Mts Dieng, (**22**) Mts Merbabu-Merapi, (**25**) Mt Lawu, (**26**) Mts Liman-Wilis, (**27**) Mt Arjuno, (**28**), Mts Kawi-Kelud, (**30**) Mts Bromo-Tengger-Semeru, (**32**) Yang plateau and (**35**) Mts Ijen-Raung

8 of which Mt Arjuno-Welirang (3,339 m.a.s.l. [27]) and Mt Semeru (3,676 m.a.s.l. [32]) are the highest. The zonation of the vegetation on the mountains of Java has been described in detail by Steenis (1972) and, for the purpose of the present study, I adopt the following classification: Lowland Zone below 1,200 m.a.s.l., the Submontane Zone between 1,200 and 1,600 m.a.s.l., the Montane Zone between 1,600 and 2,400 m.a.s.l., and the Subalpine zone above 2,400 m.a.s.l. (and up to 3,676 m.a.s.l. on Mt Semeru).

The climate on Java differs greatly from the west to the east. The eastern part of Java and the north coast have a pronounced dry season, while in the western half it is weak and nowhere marked (RePPProT 1990). The amount of rainfall varies from <1,000 mm per year in the Northeastern tip of the island at Baluran [36] to >8,000 mm on the Southeastern slopes of Mt Rogojembangan in Mts Dieng [19]. The rainfall gradients on Java can be steep: moving just 25 km north from Mt Rogojembangan, the rainfall has dropped to <2,000 mm and likewise, moving 15 km Southwest from Baluran, up Mt Ijen [35], the annual rainfall has increase to >3,000 mm (note that ebony langurs have been recorded in all the above-mentioned localities).

While the absolute amount of rainfall bears some significance for the distribution of plants and animals on Java, the length of the dry season seems to be of greater significance. In general, the wettest vegetation types (mixed lowland and hill rain forest and everest montane forest) only occur in areas with at least 30 rainy days during the driest four consecutive months (Steenis 1965), and hence is mostly found in the west and central part of Java. Rainforest is also found throughout the otherwise seasonally dry east in the wet 'islands' which arise as a result of stowage on the southern and south-eastern slopes of the higher mountains (Steenis 1972). In the drier areas rain-forest is replaced by moist forest and deciduous forest.

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Data Aquisition

I collected data on ebony langurs by conducting surveys throughout the species' range on Java, Bali and Lombok, between 1994–2003 and 2012–2013, most of which are detailed in an earlier publication (Nijman 2001); here I restrict myself to Java only. All types of forest were surveyed and included the following mountains and plateaus (listed in a west to east sequence, Fig. 1): Mt Salak (1994, 1995, 1997, 1999, 2000), Mt Gede-Pangrango (1994, 1995, 1997–2001, 2003), Mt Tangkuban Perahu (1994), Mt Papandayan (1999, 2012, 2013), Mt Slamet (1994, 1995, 1999), Mts Dieng (1994, 1995, 1997–2002), Mt Sundoro (1994), Mt Merbabu (1994), Mt Merapi (1994, 1995), Mt Lawu (1994, 1995), Mts Liman-Wilis (1994, 1995), Mt Arjuno-Welirang (1997, 1998), Mt Kawi-Kelud (1997), Yang plateau (1997), Mt Ijen (2000, 2001). Surveys typically lasted several days, with multiple sites visited and most sites being re-visited over the years. While considerable time was spent in the Submontane Zone, surveys in the Montane Zone up to 2,400 m.a.s.l. were less frequent and the area above 2,400 m.a.s.l. was surveyed mainly by several single day trips, retreating to lower elevations for the night. The total survey effort in Submontane, Montane and Subalpine Zones, in areas where ebony langurs were indeed recorded, was 177 days.

Data were collected on the occurrence and altitudinal distribution of ebony langurs, and upon sighting of an individual or a group, an estimate was made of the group size and the altitude was measured with the aid of an altimeter (either on a wrist watch or on a handheld GPS receiver).

In 10 areas from across the island, densities and group sizes of ebony langurs were estimated along transects and forest trails following the methodology and assumptions described in Nijman and Balen (1998). These areas comprised six sites in the Lowland Zone between sealevel and 800 m.a.s.l., three of which were in the wet climate zone (>20 rainy days during the four driest consecutive months) and three in the dry zone (<20 rainy days during the four driest consecutive months). Four Submontane and Montane sites between 1,300 and 2,800 m.a.s.l., were surveyed, with two in the wet and two in the dry climatic zone.

In addition to surveys I collected data on the distribution, elevation and group sizes of ebony langurs throughout Java as reported in the literature. While most of these were conducted in the lowlands they did allow me to evaluate differences between montane and lowland populations.

Analysis

I entered the locality data, at a precision of ~ 1 km^2, into a GIS model containing environmental layers comprising temperature, precipitation and altitude. The temperature and precipitation variables were extracted from the WorldClim database (Hijmans et al. 2005). These bioclimatic variables are derived from monthly temperature and rainfall values resulting in ecologically relevant layers on a grid resolution of ~1 km^2. These variables were used to explore the relationship between group size and environment, including altitude. I selected maximum group size per site as these showed the largest amount of variation across the island. I prepared a multiple linear regression model that was fitted on the (normalised) data to determine the best sub-set of environmental variables as predictors for the observed variation in maximum group sizes. The effects of collinearity were reduced by simply omitting predictor variables that correlated highly with the other predictor variables that remained in the model (Quinn and Keough 2002). The entered variable included altitude (in m.a.s.l.), annual precipitation (in mm), precipitation seasonality (reflecting the annual range in precipitation, expressed as a standard deviation) and temperature seasonality (reflecting the annual range in precipitation, expressed as a coefficient of variation). Statistical analyses were done in SPSS17 and a test was deemed significant when $P < 0.05$ in a two-tailed test (Siegel 1956).

Results and Discussion

Physical Condition of Mountains as Langur Habitats

Java is situated between 6° and 8° south of the equator, and experiences a true tropical climate. The uniformity of the temperature conditions in Java makes the differences between the climate of the higher regions and that of the low plains prominent. In addition to the decrease of temperature of about 0.6 °C for each rise of 100 m (Braak 1929), the climate also changes in other respects with increasing elevation (Whitten et al. 1996; Steenis 1972). Heat is more quickly lost from high altitudes at night, and therefore the daily temperature fluctuations are greater in the mountains than in the lowland, viz ~15–20° C (up to 25° C, see below) compared to ~5–8° C. The climate of Java's Montane Zones shows some pronounced differences between the drier east and the wetter west, which is well illustrated by two examples: Mt Bromo-Tengger-Semeru [30 in Fig. 1] and the Dieng Plateau [19]. The climate of western slopes of Mt Bromo-Tengger-Semeru at ~1,750 m.a.s.l. is characterised by large amounts of rainfall (annually ~ 1,980 mm), with a marked dry season from June to October when average monthly precipitation falls below 100 mm. The average maximum monthly temperature remains constant at ~22 °C, while the minimum monthly temperature averages ~13 °C dropping to 11 °C during the dry season. At the height of the dry season, evaporation exceeds precipitation, indicating the area (and the langurs living there) experiences an arid period. Further to the west, on the Dieng Plateau at ~2,200 m.a.s.l., the rainfall is likewise high (annually ~2,180 mm), with a short dry season from July to September when average monthly precipitation falls below 100 mm. Like at Mt Bromo-Tengger-Semeru, the average maximum

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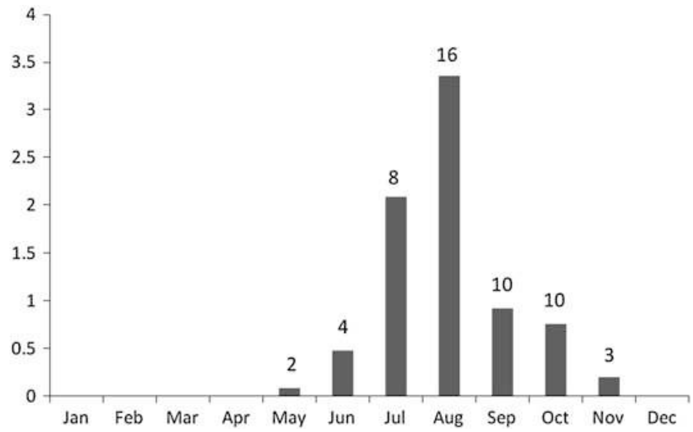

Fig. 2 Average number of frost days at Kertasarie Estate, West Java at 1,600–1,650 m.a.s.l. for the period 1909–1938. Numbers above the bars are the maximum number of days frost occurred within 1 month

monthly temperature remains constant throughout the year but, at ~19 °C, slightly lower. The average minimum monthly temperature is in the single digits, averaging 7 °C but dropping to 3–4 °C in July–September.

Since cool air is heavier than warm air, when air cools down at night, it naturally will flow down slopes. If, however, there is no slope down which it can flow, for example in hollows, valleys or plateaus, the air will get progressively colder. The Dieng Plateau, surrounded as it is by mountains on all sides, illustrates this principle well, and the temperature drops more during the night than what might be expected purely based on altitude. During the dry season, ground frost often occurs daily during these dry months.

Frost does occur, albeit irregularly, in the mountain areas of Java (Vrolijk 1934; Steenis 1968, Domrös 1976). Frosts in these areas represent a typical *local* climatological phenomenon, favored by the volcanic small-scale topography. Frost may occur at low level ('ground frost') due to nocturnal radiation especially in 'frost holes' on high mountains, or on montane plateaus surrounded by higher mountains. Frosts occur at elevations above 1,500 m in depressions only, whereas slopes—even at much higher elevation, such as close to the peak of Mt Pangrango at 3,019 m.a.s.l.—can remain frost free year-round (Domrös 1976). Given the importance of the occurrence of frost for tea cultivation, ample data are available from tea plantations. Domrös (1976) summarised data from the Kertasarie Estate in West Java situated between 1,600 and 1,650 m.a.s.l. [near 10 in Fig. 1]. Here, between 1,909 and 1,938, frost was recorded in 4 out of every 5 years, with an average of ~10 nights a year, ranging from 0 to 38 nights. Frost occurred between May and November, but with a clear peak in July and August (Fig. 2). The largest number of frost nights recorded in 1 year was 38 (in 1925), and the largest number of frost nights in 1 month was 16 (in August 1914). The largest amount of temperature variation measured on a single day (20–21 August 1923) was 25 °C, from −2 °C to +23 °C. While in most nights the temperature fell just below the freezing point, on some nights temperatures dropped until −4.0 °C to −5.6 °C. No contemporary data are available from comparable sites at equal or higher elevations, but using the general rule of a decrease of temperature of about 0.6 °C for every rise of 100 m, one can, at least during clear nights in the dry season, expect the temperature to drop to minus double digits on the highest mountains. Indeed, Steenis (1972) reported the temperature at ground level on Mt Papandayan [10] to have dropped to −10 °C.

As a general rule, in the mountains cloudiness increases as rainfall increases. On reaching higher altitudes, the intensity of the rains is reduced, but the total duration of showery weather increases. Instead of the heavy tropical cloudbursts, light showers becoming more frequent (Braak 1929). In terms of vegetation, the distinction between the Lowland Zone and the Submontane Zone is largely floristic, with several true lowland (megaterm) plant families being restricted to lower elevations, and other cold-loving (microterm) families occur only higher up. Moving from the Submontane Zone into the Montane Zone, the physiognomy of the forest changes into a closed high-stemmed forest, with decreasing stem diameter and increasing quantity of mass above 2000 m.a.s.l. In the Subalpine Zone, there is dense low forest with few emergents, often covered extensively in moss, and conifers become more common. Of course, these are the general aspects of botanical zonation and other factors may cause deviation (Steenis 1972).

Altitudinal Distribution of Langurs on Mountains

There has been some confusion regarding the altitudinal distribution of ebony langurs on Java. Bennett and Davies (1994) stated that the species is restricted to coastal and riverine habitats. Zon (1978) reported them to be present in mangrove, swamp, and lowland rainforest up to 1,500 m.a.s.l., often near human settlements. Medway (Lord 1970) considered its habitat to be inland forest from the lowlands up to almost 2,000 m.a.s.l. For Mt Gede-Pangrango, Doctors van Leeuwen (1926, 1933) reported ebony langurs to occur in the higher parts of the mountains, >2,400 m.a.s.l., while Kohlbrugge (1896) reported that he regularly observed them at altitudes up to 2,300 m.a.s.l. on Mt Semeru. Bemmel-Lenneman and Bemmel (1940) reported on the occurrence of ebony langurs in Mts Bromo-Tengger-Semeru from altitudes of 2,100 m.a.s.l. to “near the summit of the Mt Semeru”. Indeed, Veen (1940) recorded a number of ebony langurs that had died at Semeru’s summit, i.e. close to 3,676 m.a.s.l.

During the surveys, ebony langurs were indeed found in mangrove, swamp and lowland forest, along the coast and along rivers, but also throughout the mountains, both in the wetter west and the drier east. Indeed, it appears that they are found in essentially all parts of Java where there is natural forest left. Ebony langurs were observed on 16 of the 18 mountain or mountain complexes on Java

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which have their highest peaks above 2,500 m.a.s.l. (I did not find them during a short survey on Mt Sundoro in central Java in 1994 and I have no data from Sundoro's twin volcano Mt Sumbing; I found little forest remaining on Mt Sundoro but good forest may still be found on Mt Sumbing).

Given that some of the best forest areas on Java are situated in montane areas, in terms of population numbers and sizes, these areas are the stronghold for the species. Ebony langurs were observed frequently in the Montane Zone between 1,600 and 2,400 m.a.s.l., but also at higher elevations. The tree line appeared to be the natural altitudinal boundary for the species, with groups observed at the tree line, and in gnarled forest and tall shrubs but not in the open subalpine fields adjacent to the forest. The tree line on Java is not situated at a fixed altitude. It is normally located below the highest point of the mountain on active volcanoes, such as Mt Gede [6] or Mt Arjuno [27], but can reach the summit on dormant volcanoes, such as Mt Pangrango [6] or Mt Prahu in Mts Dieng [19]. It is a well-documented phenomenon, known as the Massenerhebungeffect, that the tree line is situated at considerably higher elevations on taller mountains (Steenis 1972). Indeed, on mountains such as Mt Slamet (3,432 m.a.s.l. [16]) and Mt Semeru (3,676 m.a.s.l. [32]) the forest, albeit somewhat dwarfed, extends to altitudes of well above 3,000 m.a.s.l. In the forests on these highest mountains, the highest altitude populations of the ebony langurs are found.

Groups were observed in high mountain areas during all months of the year, and at high elevation sites that were visited frequently, such as the higher parts of Mt Gede Pangrango [6] and especially Mts Dieng [19], ebony langurs were invariably present. Indeed, the permanent occurrence of ebony langurs at 2,100–2,200 m.a.s.l. in Mts Bromo-Tengger-Semeru has been noted (Bemmel-Lenneman and Bemmel 1940). As such, there is no indication that the ebony langurs migrate up and down along the elevation gradient, either daily or seasonally.

Group Sizes and Densities on Mountains

Densities and group sizes are related to both altitude and climatic conditions. Densities of ebony langurs appear to be higher in the drier forest types compared to the wet forest areas, with almost 5 groups km^{-2} in lowland deciduous forest and just over 3 groups km^{-2} in the lowland rainforest. With group sizes being considerably larger in lowland deciduous forest compared to lowland rainforests, this translates to a 2-fold difference in the number of individuals per unit area (Table 2). The differences between the four forest types are not statistically significant when comparing group densities ($\chi^2 = 0.87$, df = 1, P = 0.35) or group sizes ($\chi^2 = 1.90$, df = 1, P = 0.17) but it is when comparing individual densities ($\chi^2 = 29.08$, df = 1, P < 0.001). Individual densities in lowland deciduous forest are significantly higher than the other three habitat types combined ($\chi^2 = 26.7$, df = 1, P < 0.001), and conversely individual densities in montane rainforest are

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Table 2 Densities and group sizes of ebony langurs *Trachypithecus auratus* in 10 forest areas in Java, showing differences between wet and dry forest types and lowland and montane areas

Elevation	Population parameter	Wet climatic zone	Dry climatic zone
Lowland <800 m.a.s.l.	Density	3.30 groups km^{-2} (3 sites)	4.80 groups km^{-2} (3 sites)
	Median group size	7 individuals (18 groups)	11 individuals (9 groups)
Montane >1,300 m.a.s.l.	Density	2.35 groups km^{-2} (2 sites)	3.60 groups km^{-2} (2 sites)
	Median group size	6 individuals (6 groups)	7 individuals (11 groups)

significantly lower than the other three habitat types combined ($\chi^2 = 10.0$, df = 1, P = 0.001).

We find a similar trend when comparing ebony langur populations in montane regions, albeit less pronounced. In the drier forest types, group densities are higher and groups have a tendency to comprise more individuals. When comparing lowland and montane populations within climatic zones, it becomes clear that densities are lower in montane areas and that group sizes are smaller as well. This is especially apparent in the dry forest areas, where groups in the lowlands typically comprise over 10 individuals where they tend to be around seven individuals in the mountains.

Group Composition on Mountains

While the typical ebony langurs group contains a single adult male and a number of immature males, females and young, groups with two adult males have been recorded (Brotoisworo 1983; Kool 1989, 1993; Kartikasari 1986; this study). While these have been recorded in areas where large groups of >20 individuals occur, the two adult male groups were not always the largest groups in the area [with for instance Kool (1989) reporting groups with two adult males containing of 13 and 17 individuals, respectively]. Two adult male groups were observed at sealevel (e.g. Pangandaran, Baluran) to ~1,400 m.a.s.l. (Ijen plateau), and judging by the distribution of groups larger than ~12 individuals (see Fig. 3), it is unlikely that they occur at higher elevations. As such, it appears that in the Lowland to Submontane Zone, below 1,600 m.a.s.l., the social organisation of the ebony langur comprises uni-male and multi-male groups but in the Montane and Subalpine Zone it is uni-male only. At present, it is not known what the relationships are between the males in these two-male groups. It is quite possible that they comprise of age-graded groups in which one of the males is a younger follower (as seen in for instance Thomas' langurs *Presbytis thomasi*: Steenbeek et al. 2000) or whether males mature and breed in their natal group (as seen in for instance Phayre's langurs *Trachypithecus phayrei*: Koenig and Borries 2012). An

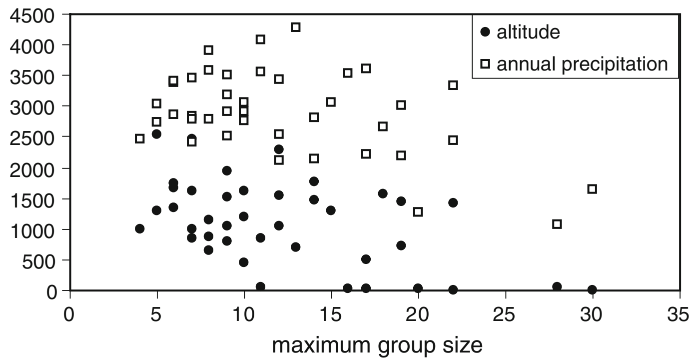

Fig. 3 Relationships between maximum group size of ebony langur *Trachypithecus auratus* and altitude (m.a.s.l.), and maximum group size and annual rainfall (in mm) for 40 sites in 27 forest areas on Java; group sizes are smaller at higher altitudes and in areas with higher rainfall

age-graded two-male group in a species that typically forms one-male units is qualitatively different from for the multi-male, multi-female groups found in, for instance, hanuman langurs *Semnopithecus* spp (Newton 1988; Koenig 2000).

I obtained data on elevation and maximum group sizes from 40 sites in 27 forest areas (24 as part of my own surveys and 3 additional ones from the literature), covering an altitudinal range between sealevel to 2,500 m.a.s.l. (these are the average altitudes of survey sites: individual groups of ebony langurs were observed at higher elevations). With respect to localities where ebony langurs were recorded there were strong correlations between altitude, precipitation and temperature variables. As expected, altitude was strongly correlated with absolute precipitation and temperature variables (Pearson's product-moment correlation coefficient, all $r > 0.316$, $P < 0.04$) but not with the seasonal variability in these variables (all $r < 0.23$, $P > 0.16$). The variability in these climatic variables decreased with altitude. At the lowland sites where ebony langurs have been recorded included sites with little seasonality in rainfall and temperature as well as sites with marked seasonality, but the mountain sites tended to be constant in terms of climatic variability. Thus, with respect to precipitation seasonality, the standard deviation equals 43 % and 40 % of the average in lowland sites ($n = 9$) and hill sites ($n = 8$) below 1,200 m.a.s.l., but only 22 % and 17 % in Submontane sites between 1,200 and 1,600 m.a.s.l. ($n = 10$) and Montane sites above 1,600 m.a.s.l. ($n = 9$), respectively. Group sizes were significantly correlated with Altitude ($r = -0.420$, $P = 0.007$), Precipitation during the Warmest Quarter ($r = -0.409$, $P = 0.009$), Precipitation Seasonality ($r = 0.468$, $P = 0.002$), and Average Annual Temperature ($r = 0.424$, $P = 0.006$).

The best model to predict the observed variation in maximum group size included precipitation seasonality and altitude. Group size increased with seasonality in rainfall, with larger groups in more seasonal regions, and group size

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Table 3 Sites where the behavioural ecology of ebony langurs *Trachypithecus auratus* has been studied, showing that most work has been done at low elevations and mostly in areas with, for Javanese standards, low amounts of rainfall and marked dry seasons. Numbers between brackets refer to Fig. 1

Province site	Duration (months)	Habitat	Elevation (m.a.s.l.)	Rainfall (mm/year)	References
West Java					
Cikepuh [5]	?	Rainforest (coastal)	0–225	3,450	Ladjar and Simanjuntak (1994)
Muara Gembong [7]	8	Mangrove (coastal)	0–10	1,650	Supriatna et al. (1989)
Mt Gede-Pangrango [9]	11	Rainforest (inland)	1,450	3,400	Beckwith (1995)
Pangandaran [14]	12	Teak/rainforest (coastal)	0–50	3,350	Kool (1989, 1993)
Central Java					
Mts Dieng [19]	5	Rainforest (inland)	600–1,600	4,300	Nijman and Balen (1998), Nijman and Nekaris (2012)
Cepu [24]	13	Teak forest (inland)	50–150	1,800	Djuwantoko (1991)
East Java					
Mt Semeru [30]	6	Rainforest (inland)	1,300–1,600	3,500	Subarkah et al. (2011)
Baluran [36]	6	Deciduous forest (coastal)	0–10	1,050	Kartikasari (1986)
Bali					
Bali Barat [opposite 36]	19	Deciduous forest (coastal)	10–100	1,500	Vogt (2003)

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decreased with increasing altitude. In all this model explained some 50 % of the observed variation in maximum group size ($F_{1,37} = 19.24$, $P < 0.001$, $R^2_{adj} = 0.48$).

1. ***Ebony langur mountain ecology***

A number of studies have been conducted on the ecology of ebony langurs, but the longer studies have been mostly at low elevations (Table 3). At least three studies have been conducted at the same site, Pangandaran. Pangandaran is a small protected area (5.2 km^2) located on a peninsula on the south coast of West Java. The highest peak on the peninsula is a mere 150 m.a.s.l., but the three research teams studied ebony langurs (Brotoisworo 1983; Kool 1989, 1993; Megantara 1994) all worked in the same coastal strip. Pangandaran is extensively used as a tourists resort, large parts of the area are covered with Teak *Tectona grandis* stands and the behaviour and ecology of ebony langurs inhabiting the part of the reserve where the studies have been conducted are likely to be influenced by the more than one million domestic and foreign tourists that visit the reserve each year. The ubiquitous presence of humans in the area may have resulted in reduced predation pressure and an increase in density of the ebony langurs. Brotoisworo (1983) started working in the area in 1976, habituating seven groups in an area of 0.8 km^2. In 1984, Kool (1989, 1993) spend a year studying two groups at Pangandaran, with home ranges between $\sim$ 0.06 and $\sim$ 0.09 km^2. Extrapolating from the data from Brotoisworo and Kool the population density reaches some 185–195 langurs km^{-2}. Comparing the densities in these areas with those found in the montane areas, as reported above, show that indeed densities are considerably lower in the mountains.

The feeding behaviour of ebony langurs has been studied in detail at six sites (Kartikasari, 1986, Supriatna et al., 1988, Brotoisworo & Dirgayusa, 1991, Kool, 1989, 1993, Djuwantoko et al. 1994; Beckwith 1995; Vogt 2003) often partially in teak plantations, and all but one (Beckwith 1995 from Mt Gede-Pangrango) at low elevations. Like all colobines, ebony langurs possess a fore-stomach digestive system, which allows them to break down cellulose. The fore-stomach microbes have a considerable potential to detoxify alkaloid defence chemicals in plant tissues. This enables the species able to cope with a substantial amount of foliage in their diet, but restricts the use of ripe fleshy fruits (Bennett 1983; Davies 1991; Kay and Davies 1994; Cork 2006; Nijman 2012). Ripe fruits, due to their high sugar content, are largely avoided and when fruit is eaten it is mostly unripe (Kool, 1989; Kartikasari 1986). Indeed, a large part of the diet of ebony langurs consists of leaves, although it varies based on habitat type and seasonality. The amount of foliage in the diet ranges from 46 to 58 % (Vogt 2003), 49 to 51 % (Kool, 1989), 56 % (Kartikasari 1986), 59 % Supriatna et al. (1988), 64 % (Beckwith 1995), 94 % (Djuwantoko et al., 1994).

The ability of this species to cope with considerable amounts of leaves in their diet allows the ebony langurs to live in a large variety of forest types, ranging from freshwater swamps and mangrove forests to the montane forests, and from the everwet rain forest to dry deciduous forests. Ebony langurs seem to be able to cope with some habitat disturbance and to survive in secondary forest types as well as some man-made forests as pine and teak plantations (e.g. Kool, 1993, Brotoisworo, 1983, Djuwantoko et al., 1994; Nijman 2000) Often, however, these plantations are situated adjacent to other more natural forest areas, or are intersected by (river) valleys with a more diverse forest type; areas on which the species seems to depend as well. Fruit production in the montane forest, especially of fruits available for langurs, is lower than in the lowlands (Whitten et al. 1996; Van Steenis 1972). As indicated by the high proportion of leaves in the diet in Mt Gede-Pangrango, as studied by Beckwith (1995), and even more so as suggested by the study of Djuwantoko et al. (1994), it appears that the ebony langurs are indeed able to persist on leaves only. While no data are available on the diet of ebony langurs in the Montane or Subalpine Zone (i.e. above the 1,450 m.a.s.l. where Beckwith observed his study group), we can expect these populations to be amongst the most folivorous.

Conclusions

Ebony langurs do occur in high elevation forest with resident populations present between altitudes of 2,500 and 3,500 m.a.s.l., depending on the height of the mountains. This makes them the only truly tropical high mountain colobine.

Climatic conditions in the mountains of Java are distinctly different from the lowlands, with in regular occurrence of frost, larger variations in day-and-night temperature, and frequent rain. Temperatures at these altitudes average in single digits and are more reminiscent of temperate regions than the tropics.

Situated close to the equator Java experiences small climatic differences over the year, and groups of ebony langurs are present year round at these high altitudes. There are no indications that groups migrate up-and-down the mountain slopes in response to seasonal changes.

Maximum group sizes are related to altitude and seasonality in rainfall, with the largest groups in highly seasonal deciduous lowland forest and the smallest groups in high-altitude rainforest. The social organisation of ebony langurs in the mountains is restricted to single adult male groups only.

Despite important insights gained in the ecology of ebony langurs in the last 30 years since Brotoisworo's first detailed study of the species, there is a clear need for more detailed long-term studies in montane regions. This will allow a better comparison of the species' socio-ecology and population dynamics in areas under different climatic regimes.

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