

Calling patterns of Western purple-faced langurs (Mammalia: Primates: Cercopithecoidea: *Trachypithecus vetulus nestor*) in a degraded human landscape in Sri Lanka

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Abstract

The study of calling patterns is a useful non-invasive method for determining population densities and the taxonomic relationships of rare or cryptic animal species. The Western purple-faced langur *Trachypithecus vetulus nestor*, endemic to Sri Lanka's lowland rainforests, is severely impacted by forest fragmentation, with most remaining populations living almost completely in home gardens. Due to their shy nature, little is known about the behaviour of this subspecies; analysing the regular loud calls emitted by these langurs could allow for improvement of census techniques, clarification of their taxonomy, and an understanding of the impact of forest destruction on their behaviour. In 2007, we recorded the calling patterns of five male *T. v. nestor* at Talangama Wetlands. Time, duration, weather conditions, and stimulant of 253 calls were noted. Loud calls comprised three structural units: harsh barks, whoops and residuals. The average call contained 4 phrases and 3.8 residuals, was 38 seconds in length, had an average maximum frequency of 3.5 kHz, a formant frequency of 0.36 kHz, and a fundamental frequency of 0.2 kHz. Significant differences were found between individuals for the number of phrases and residuals within a call, two different phrase lengths, the formant frequency and the fundamental frequency. The earliest call occurred at 05:27 hrs, while the latest was made at 17:57 hrs. The greatest percentage of calls (73.5%) was heard in the morning (05:00-09:59 hrs), mostly stimulated by territorial battles with neighbouring troops. These results show that vocalisations can be used to distinguish individual males; as langurs are more often heard than seen, and most troops contain only a single adult male, vocalisations may be used to determine the number of troops in an area. Calls of this taxon also differed from the other subspecies, suggesting that they may be used to distinguish subspecies and their boundaries. Finally, calling behaviour differed from other subspecies. Deforestation may be a direct cause of different calling patterns. These baseline data form a valuable starting point for further studies of this Critically Endangered primate.

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Introduction

Vocalizations may serve to locate group members, alert group members of predators, convey behavioural states, attract mates or defend territories. Previous studies on vocalizations have concentrated on a wide range of species including birds (Nottebohm, 1972; Shutler and Weatherhead, 1990; Temeles, 1990; Confer, 1992; Langmore *et al.*, 1996; Langmore and Davies, 1997; Penteriani, 2003; Hall, 2004), frogs (Gerhardt, 1994), cetaceans (Janik and Slater, 1998) and primates (Zuberbuhler *et al.*, 1997; Geissmann, 2000; Kitchen, 2004; Braune *et al.*, 2005).

Amongst primates, vocalization studies are becoming more important for conservation management, particularly for rare species that are difficult to observe directly. Vocalization studies are particularly useful and important as they offer a non-invasive approach allowing for both estimating population densities, and determining taxonomic identification of un-habituated individuals (Nietsch, 1999; Zimmermann *et al.*, 2000; Ross and Geissmann, 2007). Two important methodologies include using vocalizations to survey primates by estimating numbers of groups through triangulation (Estrada *et al.*, 2003; Geissmann and Nijman, 2006; Aldrich *et al.*, 2008) or numbers of individuals by their unique vocal signatures (Boinski and Mitchell, 1997; Steenbeek and Assink, 1998; Kojima *et al.*, 2003). A third method uses vocalizations as a tool for distinguishing taxonomic variation between species or subspecies (Haimoff and Gittins, 1985; Konrad and Geissmann, 2006). The relative stability of the structural

units in primate vocal patterns (Kummer, 1970), due to their resistance to alteration by their environment (Doyle, 1978), allows for direct comparison between individuals, populations and subspecies. This feature is essential when assessing phylogenetic relationships (Struhsaker, 1970; Hohmann, 1989). Before such studies are conducted, however, it is vital that the basic vocal parameters of a species are determined (Brockelman and Ali, 1987).

The purple-faced langur (*Trachypithecus vetulus* spp.) is a highly vocal primate endemic to Sri Lanka. Adult males are the most vocal of all age and sex classes, giving characteristic loud ‘whoop’ calls (Hohmann, 1990). Similar to male grey langurs (Ripley, 1967), Nilgiri langurs (Poirier, 1970), howler monkeys (Altmann, 1959; Chivers, 1969) and gibbons (Geissmann, 2002), male purple-faced langurs emit a daily morning loud ‘whoop’ call as well as additional whoop calls throughout the day (Hohmann, 1990). Morning whoop calls are usually given shortly after sunrise and function to alert neighbours of group presence (Ripley, 1967). In comparison, whoop calls given later in the day aid in territory defence and are often accompanied by intense locomotive displays (Manley, 1986; Hohmann, 1990).

Four subspecies of purple-faced langur (*T. v. vetulus*, *T. v. philbricki*, *T. v. monticola*, *T. v. nestor*) are currently recognised, with a fifth subspecies (*T. v. harti*) postulated based on museum specimens (Deraniyagala, 1955; Nekaris and de Silva, 2008). The Critically Endangered Western purple-faced langur (*T. v. nestor*) (Fig. 1) is not only the least

studied of these taxa (Eudey *et al.*, 2006), but is also listed as one of the ‘Top 25 Most Endangered Primates’ (Mittermeier *et al.*, 2006).

With less than 3% of its original habitat remaining, *T. v. nestor* is found almost exclusively in home gardens, making traditional line transects an unfeasible method to track its dwindling populations (Rudran, 2007; Parker *et al.*, 2008). Furthermore, the exact limits of its geographic distribution are unknown (Dela, 2007), yet comparative vocal studies may offer a systematic means to confirm and classify subspecies at their boundaries.

Also of significance to the Western purple-faced langurs are the affects of increased human-wildlife conflict, decreased home range availability and increased encounters with neighbouring troops (Dela, 2004; Eschmann, 2007). By comparing factors such as call times, reasons for calling and number of calls per day between troops ranging in areas of different degrees of forest fragmentation and human population levels, it may be possible to assess the impact and the potential threat that human activity is having on purple-faced langurs (Nijman, 2001).

Although descriptive data are available regarding the male vocalizations of *T. v. philbricki* and *T. v. monticola* (Manley, 1986; Hohmann, 1990), as well as some qualitative data on *T. v. vetulus* (Douglas, 2006), no data have been published on the calls of *T. v. nestor*. Here, we quantitatively describe the calls of these langurs for the first time based on a short but intensive study of six troops at Talangama Wetlands, Sri Lanka. We also address several questions. Can whoop calls be used to distinguish males? What environmental and anthropogenic variables influence calling patterns? Can call parameters be used to distinguish the different taxa of purple-faced langurs?

Methods

Data collection took place in May and June 2007 in the Talangama Wetlands (79°55’-79°60’E and 6°53’-6°56’N) in south western Sri Lanka. Opportunistic recording of vocalizations occurred between 05:00 hours and 18:30 hours, six days a week, for seven weeks. The date, time, location, age and sex of the vocalizing individual, and the call stimulant (dawn call, induced by other monkeys, induced by human disturbance, or weather) were noted. We collected data on five adult males: A, B, G, L, and P.

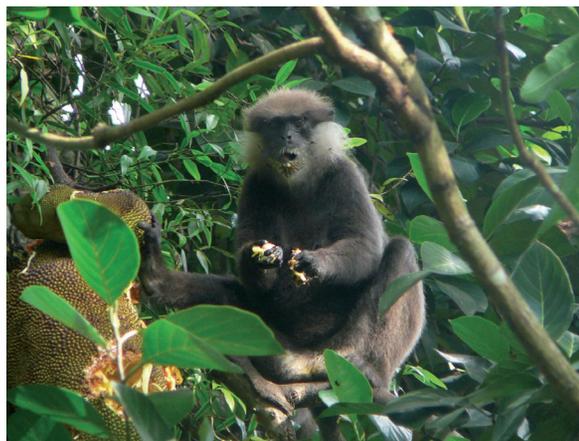


Fig. 1. Sub-adult male Western purple-faced langur eating a jack fruit in a home garden in the Talangama Wetlands; an almost total loss of forest habitat has resulted in this taxon's classification of Critically Endangered (photo by R. Moore).

Only the loud calls of the adult alpha male of each troop were recorded and analyzed. Calls were excluded that were distorted, too faint or disturbed by external and environmental noise, leaving 53 loud calls for analysis (A: $n = 10$, B: $n = 13$, G: $n = 9$, L: $n = 11$, P: $n = 10$).

Call terminology was adopted from Struhsaker (1967). A unit was defined as the simplest tonal element in a purple-faced langur call. Units may be either biphasic or monophasic (Hohmann, 1990); biphasic units were comprised of a tonal exhalation and inhalation section, while monophasic units were exhalation tones only. Units grouped together form a phrase; two or more phrases were separated by a time interval greater than any intra-unit intervals. A bout was comprised of several phrases joined by intra-phrase intervals. Residuals, which were monophasic and biphasic units occurring in between phrases, were also measured (Douglas, 2006).

We used a Marantz PMD 222 portable cassette recorder, an Audio-Technica AT897 shotgun microphone and TDK 90 minute D IEC I/TYPE 1 tapes to record vocalizations. The structural features of purple-faced langur calls were analyzed using Avisoft-SASLab Pro version 4.0 acoustic software. The calls were recorded in a hamming window with an FFT length of 256 points, a sampling bit of 16 and a bandwidth of 224 Hz. The sampling rate ranged from 4.00 kHz to 11.025 kHz. The resolution was 172 Hz. Once inputted, vocalizations were then displayed as oscillograms and spectrograms. Calls were

analyzed for distinguishing vocal patterns as well as call duration, number of phrases, number of residuals, length of phrases and length of inter-phrase intervals. The number of units per phrase and per residual were calculated, as were the maximum frequency, the formant frequency and the fundamental frequency for each call.

The Kruskal-Wallis one way analysis by ranks and the Mann-Whitney U-test were applied to the data. Significance was accepted when $p < 0.05$ in a two-tailed test (Zar, 1999).

Results

The parameters of 54 analysed calls are summarised in Table 1.

The greatest amount of variation within each individual was in the length of calls, while the parameters with the lowest deviation from the mean were the formant frequency and the fundamental frequency. Loud calls comprised three different structural units: harsh barks, whoops and residuals (Figure 2).

All loud calls began with a single harsh bark followed by a series of whoop units. Remaining phrases either began with another harsh bark or a crescendo of whoop units. Variation in the structure of the call also lay within the inter-phrases intervals. Although residuals commonly occurred in between phrases, both monophasic and biphasic harsh barks

Table 1. Descriptive statistics of all recorded whoop calls, showing particular variation in call length and number of residuals.

	Number	Range	Minimum	Maximum	Median	Mean	Std. Deviation
Length of call (seconds)	48	89.35	2.92	92.27	34.35	38.40	15.57
Number of phrases	48	7.00	1.00	8.00	4.00	4.02	1.39
Number of residuals	48	9.00	0.00	9.00	3.00	3.81	1.84
Maximum frequency kHz	54	3.56	1.82	5.38	3.50	3.52	0.81
Formant frequency kHz	54	0.12	0.29	0.41	0.37	0.36	0.03
Fundamental frequency kHz	54	0.16	0.13	0.29	0.19	0.20	0.03

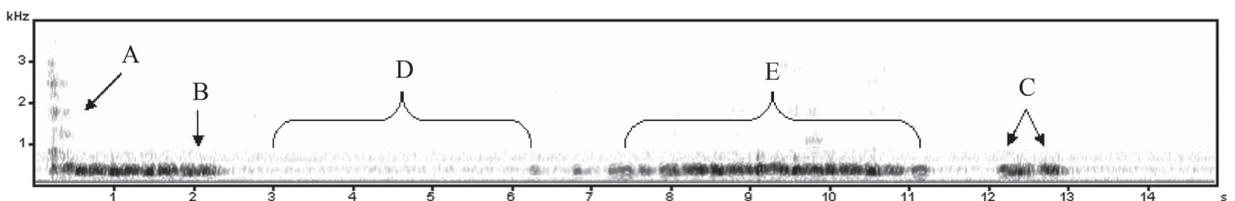


Fig. 2. Spectrogram of a male G loud call. Call patterns are: (A) harsh bark, (B) whoop units and (C) residual units. The inter-phrase interval is depicted by (D), while (E) illustrates a phrase.

were also observed. Residuals never occurred after the first phrase and always occurred after the second phrase.

Using Kruskal-Wallis tests, significant differences were found between individuals A, B, G, L and P for the number of phrases within a call ($H = 14.41$, $df = 4$, $p < 0.01$), the number of residuals within a call ($H = 15.25$, $df = 4$, $p < 0.01$), the formant frequency ($H = 29.34$, $df = 4$, $p < 0.001$) and the fundamental frequency ($H = 10.70$, $df = 4$, $p < 0.05$). In comparison, the length of each call and the maximum frequency of each call were not significantly different between individuals (Table 2).

Lengths of phrases were also compared between individuals. Only those calls that contained the particular phrase in question were compared; those missing that phrase were removed from the data sample. Only phrases 1 ($H = 27.89$, $df = 4$, $n = 46$, $p < 0.001$), 2 ($H = 14.95$, $df = 4$, $n = 45$, $p < 0.01$) and 4 ($H = 10.3$, $df = 4$, $n = 27$, $p < 0.05$) showed significant differences between individuals A, B, G, L and P. Phrases 1 and 2 were subjected to a pairwise comparison between individuals. Mann-Whitney U-tests revealed that significant differences exist between at least one phrase length of all individuals except male L and male P (Table 3).

	B	G	L	P
A number of phrases	-0.3	-2.62*	-1.29	-2.65**
number of residuals	-0.94	-1.81	-0.84	-1.93
formant freq.	-2.26*	-3.63***	-1.23	-3.05**
fundamental freq.	-2.08*	-2.45*	-1.56	-0.86
B number of phrases		-2.39*	-1.06	-2.55*
number of residuals		-2.84**	0.00	-1.83
formant freq.		-3.83***	-1.49	-1.78
fundamental freq.		-.23	-0.92	-1.84
G number of phrases			-1.89	-0.62
number of residuals			-2.29*	-3.38***
formant freq.			-3.54***	-3.58***
fundamental freq.			-1.47	-2.57*
L number of phrases				-2.01
number of residuals				-1.32
formant freq.				-2.42*
fundamental freq.				-1.05

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

	B	G	L	P
A phrase 1	-2.89**	-0.48	-2.58**	-2.26*
phrase 2	-0.37	-2.6**	-1.59	-0.11
B phrase 1		-3.67***	-1.62	-3.18***
phrase 2		-2.74**	-2.13*	-0.62
G phrase 1			-3.43***	-3.47***
phrase 2			-3.05***	-2.02*
L phrase 1				-1.29
phrase 2				-1.35

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

	Number	Earliest call	Latest call	Mean number of calls per day
A	29	05:43	16:54	2
B	23	05:27	15:00	2
G	22	05:33	14:31	4
L	23	05:33	16:00	2
P	15	05:35	13:01	3

* individual not followed in afternoon

Table 2. The results of Mann-Whitney U-tests on call variables, showing differences between each pair of adult males for each call parameter; all of these characters contribute to distinguishing individuals by their calls alone.

Table 3. Mann-Whitney U-test results showing the differences in the first and second phrase lengths between each pair of individual males, A, B, G, L and P. Phrase length appears to be a good character for distinguishing individuals.

Table 4. This table shows times of earliest and latest calls of followed males. *T. v. nestor* calls earlier than other subspecies, perhaps due to limited canopy cover in its highly disturbed habitat, which allows sunlight to penetrate more easily.

Of 253 noted calls (including individuals not followed), the earliest occurred at 05:27 hrs and was the morning call of adult male B, while the latest was made at 17:57 hrs by an unknown individual. Table 4 lists the earliest and latest loud calls exhibited by each followed male as well as the average number of calls produced per day. The greatest percentage of calls (73.5%) was heard in the morning hours (05:00-09:59 hrs), with a steady decrease in numbers (16.6%) during midday (10:00-13:59 hrs) and afternoon (9.9%: 14:00-17:59 hrs). There were no significant differences between the time of day (morning/afternoon/evening) in which males A, B, G, L, and P called ($H = 6.77$, $df = 5$, $p > 0.05$).

The percentage of calls induced by each stimulant was calculated from 118 vocalizations. Other neighbouring troops of purple-faced langurs were the main stimulant for calling, with 56.7% of noted calls being caused by outside troops. Dawn induced calls held the second highest position (21%), as all monkeys followed produced the stereotypical morning call. Human (6.1%), aggression (5%) and weather (2%) induced calls as well as calls in which it was impossible to discern what stimulated calling (unknown = 9.2%) were minimal. There were no significant differences among what stimulated individuals A, B, G, L and P to call ($H = 8.58$, $df = 5$, $p > 0.05$).

Adult males called in all types of weather. Figure 3 compares the percentage of calls ($n=253$) heard in each type of weather with the percentage of time spent in each weather condition. Calls were most often heard when it was partly cloudy (30.4%) or overcast (28.9%).

Although calls did occur when it was raining (0.8%), they were relatively few. Seventeen percent of calls took place when it was sunny, while 14.6% of calls were during twilight and 8.3% were when it was drizzling. There were no significant differences between the individuals who called and the weather conditions in which they called ($H = 11.67$, $df = 7$, $p > 0.05$).

Discussion

The loud calls of adult male Western purple-faced langurs are similar in structure, function and distribution throughout the day to those of other colobines (Ripley, 1967; Poirier, 1970; Marler, 1972; Vogel, 1973; Horwich, 1976; Oates and Trocco, 1983;

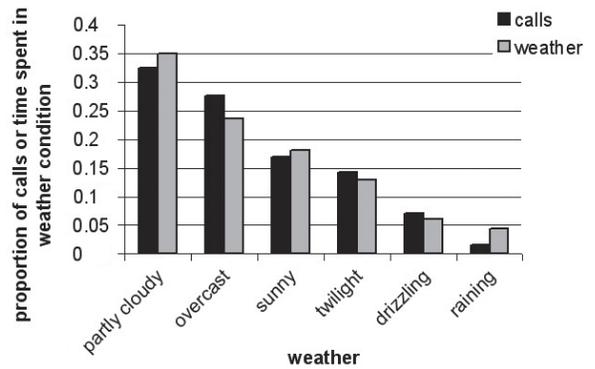


Fig. 3. Western purple-faced leaf monkeys called during all weather conditions. This figure shows the percentage of calls heard during specific weather conditions ($n = 253$) compared to the percentage of time they spent in each weather condition ($n = 432$ hrs).

Herzog and Hohmann, 1984; Hohmann, 1989). The calls comprised characteristic acoustic units. Analyses of the organisation of tonal units revealed a common syntax structure between individuals, as well as individual differences. These calling patterns are comparable to those documented for the subspecies *T. v. philbriki* (Hohmann, 1990), *T. v. monticola* (Manley, 1986; Hohmann, 1990) and *T. v. vetulus* (Douglas, 2006).

The frequencies of Western purple-faced langur calls are well-adapted for optimal propagation over long distances. Calls with frequencies ranging from 0.10-1.00 kHz propagate well, while calls with frequencies near 0.2 kHz have low attenuation rates (Waser and Waser, 1977; Wiley and Richards, 1978; Wiley and Richards, 1982; Waser and Brown, 1986). The frequency range of *T. v. nestor* in Talangama Wetlands was 0.13-5.38 kHz. Although the maximum observed frequency is much higher than the previously reported optimal frequency range, these measurements were taken from the harsh barks within a call. In addition, because of the repetitive nature of the whoop units that make up the bulk of purple-faced langur loud calls, encoded information is thought to degrade slowly, thus allowing intact messages to travel further distances before losing their content (Wiley and Richards, 1978; Wiley and Richards, 1982; Waser and Brown, 1986). The average formant frequency of *T. v. nestor* calls was 0.36 kHz. This frequency, which has been observed in a variety of primate species (Struhsaker, 1970; Oates and Trocco, 1983), is believed to interact minimally

with reverberation and ambient noise (Waser and Brown, 1986). Given the large differences observed between the frequencies of the harsh barks and the whoop units, it is possible that the harsh bark functions to transmit information to individuals relatively close by, while the whoop units transmit information to individuals further away.

Loud calls are useful in distinguishing individual purple-faced langurs. Significant differences between individuals A, B, G, L and P were found in the number of phrases per call, the number of residuals per call, the formant frequency and the fundamental frequency. Based on these findings, it is possible to deduct that information regarding the caller's identity, location and behavioural state is contained within these call parameters (Busnel, 1977; Cowlshaw, 1996). Distinctiveness of calls can also facilitate future survey efforts, allowing researchers to detect groups based on calls alone (Geissmann *et al.*, 2005). In addition loud calls of other primates are known to contain specific information regarding the physical fitness of the caller, the size of the troop and the presence or absence of young (Wilson *et al.*, 2001; Kitchen, 2004). It is possible that the differences observed in the calls of the males in this study were the result of individually distinctive messages regarding troop composition and fitness encoded into the loud calls.

Although troops were followed from dawn till dusk, there was a marked difference in the numbers of calls heard throughout the day, with the fewest calls occurring in the evening. The majority of calls were observed in the morning and correlated with increased activity levels during that period (Eschmann, 2007). This is consistent with findings for the other subspecies (Hohmann, 1990; Douglas, 2006) as well as with other colobines (Ripley, 1967; Poirier, 1970; Chivers, 1973; Vogel, 1973; MacKinnon, 1974; Horwich, 1976; Herzog and Hohmann, 1984; Hohmann, 1989), cebids (Altmann, 1959; Horwich and Gebhard, 1983), titi monkeys (Aldrich *et al.*, 2008), and lesser apes (Chivers, 1973; MacKinnon, 1974; Geissmann, 2002; Geissmann and Nijman, 2006; Konrad and Geissmann, 2006). Increased calling in the morning hours may be the result of optimal calling conditions. A combination of warmer air above the tree canopy and cooler air below it acts as a reflector of sound, increasing the intensity of the call at further distances (Waser and Waser, 1977; Wiley and Richards, 1978).

Although environmental characteristics certainly impact calling times, anthropogenic disturbance also seems to play a role. The earliest morning call of *T. v. nestor* was heard at 05:27 hrs, which was half an hour before sunrise, later than reported by Ripley (1967) for the species as a whole. The latest morning call occurred at 06:25 hrs. The majority of calls were heard prior to the technical sunrise, in conjunction with the first detectable signs of the sun. Daily human activities did not appear to affect the timing of morning calls, as calls were not dependent on the levels of noise from neighbouring homes (Eschmann, 2007). In comparison, the majority of *T. v. vetulus* morning calls occurred post-dawn when the sun had fully penetrated to the forest floor (Douglas, 2006). The fact that *T. v. nestor* calls before sunrise may be related to the meagre canopy continuity in the Talangama Wetlands. Most trees have been cut down to make room for housing developments; the few that remain occur in fragmented belts throughout the villages (Eschmann, 2007). Because of this, much of the monkeys' home ranges are exposed to direct sunlight.

Loud calls of colobines are thought to function in the maintenance of a troop's territory (Eisenberg *et al.*, 1972). Similar to findings regarding *T. v. philbriki* and *T. v. monticola* (Hohmann, 1990), the majority of the loud calls of *T. v. nestor* were induced by sunrise and neighbouring troops of monkeys. Morning calls are believed to space troops, while daytime calls are thought to aid in the defence of home ranges (Ripley, 1967; Eisenberg *et al.*, 1972; Manley, 1986; Hohmann, 1990). As purple-faced langurs are extremely territorial (Ripley, 1967; Manley, 1978; Manley, 1986; Nekaris and de Silva Wijeyeratne, 2008), these results are not surprising. As observed in other primates (e.g. Kitchen, 2004), two or more neighbouring alpha males commonly responded directly to the loud calls of each other with their own loud call. This calling pattern is ideal for triangulation studies (Estrada *et al.*, 2003), providing yet another non-invasive method to estimate much-needed population densities of these monkeys in a highly fragmented urban landscape (Rudran, 2007).

Human activity seemed to have little effect on the calling behaviours of langurs in the Talangama Wetlands. Although people often came into contact with troops of monkeys, the monkeys rarely responded. In fact, monkeys were so desensitized to humans that they often refused to move from feeding trees

even when they were being verbally threatened or when rocks were thrown at them. All human-induced loud calls were the direct result of interactions with the unfamiliar researchers and not the locals. Airplanes and vehicles, which have been previously reported to induce loud calls (Hohmann, 1990; Dela, 2007), elicited no response from Western purple-faced langurs. The consequence of living in such a highly urbanized environment has desensitised the langurs to the effects of most human activity.

Although loud calls were recorded under a variety of weather conditions, the majority of calls were observed when the weather was either cloudy or overcast. Horwich (1976) has reported a significant preference of Nilgiri langurs (*T. johnii*) for calling when the weather is cloudy and misty. The data regarding weather and calling patterns of langurs in this study do not necessarily reflect a preference for vocalizing under cloudy conditions, but more likely reflect that the study took place during the monsoon season. In order to depict more accurately how weather influences call patterns and distribution throughout the day, further research should be conducted during non-monsoon periods. Decreased occurrences of calls during the rain may stem from the fact that rain decreases propagation and increases attenuation of calls (Wiley and Richards, 1978), suggesting that vocal studies must not exclude days affected by monsoon rains when assessing the impact of weather on the vocal repertoire of purple-faced langurs. Most studies that use primate calls to estimate densities exclude rainy days (Brockelman and Ali, 1987; Buckley *et al.*, 2006); such methods should be reconsidered when estimating small and fragmented populations of purple-faced langurs.

In this study we have provided evidence that purple-faced leaf monkey calls are distinct amongst individual males; this combined with their ritualised morning occurrence makes them ideal for future survey work of this Critically Endangered subspecies. Quantitative differences between taxa are also evident, and future work should not only aim to compare the calls of all four recognized subspecies (*T. v. nestor*, *T. v. vetulus*, *T. v. philbriki* and *T. v. monticola*), but also the calls of individuals who are suspected of being *T. v. harti*. This type of comprehensive study would ultimately validate the existence of the fifth postulated subspecies, while also providing a means for determining the boundaries of each subspecies. As human encroachment on their habitat continues, langurs are being forced

into smaller ranges. Long-term studies of *T. v. nestor* should address the impact of habitat reduction on the vocal behaviour of this highly territorial taxon.

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References

- Aldrich B, Molleson L, Nekaris KAI. 2008. Vocalizations as a conservation tool: an auditory survey of the Andean titi monkey *Callicebus oenanthe* Thomas, 1924 (Mammalia: Primates: Pitheciidae) at Tarangue, Northern Peru. *Contributions to Zoology* 77: 1-6.
- Altmann SA. 1959. Field observations on a howling monkey society. *Journal of Mammalogy* 40: 317-330.
- Bearder SK, Honess PE, Ambrose L. 1995. Species diversity among galagos with special reference to mate recognition. In: Alterman L, Doyle G, Izard MK, eds. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum, 331-352.
- Boinski S, Mitchell CL. 1997. Chuck vocalizations of wild female squirrel monkeys (*Saimiri sciureus*) contain information on caller identity and foraging activity. *International Journal of Primatology* 18(6): 975-993.
- Braune P, Schmidt S, Zimmermann E. 2005. Spacing and group coordination in a nocturnal primate, the gold brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. *Behavioral Ecology and Sociobiology* 58(6): 587-596.
- Brockelman WY, Ali R. 1987. Methods of surveying and sampling forest primate populations. In: Marsh CW, Mittermeier RA, eds. *Primate conservation in the Tropical Rain Forest*. New York: Alan R. Liss Inc., 23-62.
- Buckley C, Nekaris KAI, Husson SJ. 2006. Survey of *Hylobates agilis albibarbis* in a logged-peat swamp forest: Sabangau catchment, central Kalimantan. *Primates* 47(4): 327-335.
- Busnel R. 1977. Acoustic communication. In: Sebeok TA, ed. *How Animals Communicate*. Bloomington: Indiana University Press, 233-251.

- Chivers D. 1969. On the daily behaviour and spacing of howling monkey groups. *Folia Primatologica* 10: 48-102.
- Chivers D. 1973. An introduction to the socio-ecology of Malayan forest primates. In: Michael RP, Crook JH, eds. *Comparative Ecology and Behaviour of Primates*. New York: Academic Press, 101-146.
- Confer JL. 1992. Golden-winged warbler, *Vermivora chrysoptera*. In: Schneider KL, Pence DM, eds. *Migratory non-game birds of management concern in the Northeast*. Massachusetts: United States Fish and Wildlife Service, 369-383.
- Cowlshaw G. 1996. Sexual selection and information content in gibbon song bouts. *Ethology* 102: 272-284.
- Deraniyagala PE. 1955. A new race of leaf monkey from Ceylon. *Spolia Zeylanica* 27: 293-294.
- Dela J. 2004. Protecting the endemic purple-faced langur. *Loris* 23(5-6): 14-22.
- Dela J. 2007. Seasonal food use strategies of a colobine frugivore, *Trachypithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. *International Journal of Primatology* 28(3): 607-626.
- Douglas PH. 2006. *Microhabitat Variables Influencing Abundance and Distribution of Primates (Trachypithecus vetulus vetulus and Macaca sinica aurifrons) in a Fragmented Rainforest Network in Southwestern Sri Lanka*. M.Sc. thesis, Oxford, UK: Oxford Brookes University.
- Doyle GA. 1978. Discussion of behavioural factors in prosimian evolution. In: Chivers DJ, Joysey KA, eds. *Recent Advances in Primatology, Vol. 3*. London: Academic Press, 151-157.
- Eisenberg JF, Muckenhirn NA, Rudran R. 1972. The relation between ecology and social structure in primates. *Science* 176(4037): 863-874.
- Eschmann C. 2007. *An Investigation into the Calls and Behaviours of Western Purple-Faced Leaf Monkeys (Trachypithecus vetulus nestor) in a Suburban Environment: a Case Study from the Talangama Wetlands, Sri Lanka*. M.Sc. thesis, Oxford, UK: Oxford Brookes University.
- Estrada A, Luecke L, van Belle S, Barrieta E, Rosales-Meda M. 2003. Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. *Primates* 45: 33-39.
- Eudey A, Members of the Primate Specialist Group 2006. *Trachypithecus vetulus*. 2006 IUCN Red List of Threatened Species. <http://www.iucnredlist.org> (27 February 2007).
- Geissmann T. 2000. Gibbon songs and human music from an evolutionary perspective. In: Wallin NL, Merker B, Brown S, eds. *The Origins of Music*. Massachusetts: MIT Press, 103-123.
- Geissmann T. 2002. Duet-splitting and the evolution of gibbon songs. *Biological Review* 77: 57-76.
- Geissmann T, Bohlen-Eyring S, Heuck A. 2005. The male song of the Javan silvery gibbon (*Hylobates moloch*). *Contributions to Zoology* 74(1/2): 1-25.
- Geissmann T, Nijman V. 2006. Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): behavior, phylogeny, and conservation. *American Journal of Primatology* 68: 1-19.
- Gerhardt HC. 1994. Reproductive character displacement of female mate choice in the gray tree frog *Hyla chrysoscelis*. *Animal Behaviour* 47: 959-969.
- Haimoff EH, Gittins SP. 1985. Individuality in the songs of wild agile gibbons (*Hylobates agilis*) of Peninsular Malaysia. *American Journal of Primatology* 8: 239-247.
- Hall ML. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology* 55: 415-430.
- Herzog MO, Hohmann G. 1984. Male loud calls in *Macaca silenus* and *Presbytis johnii*. *Folia Primatologica* 43: 189-197.
- Hohmann G. 1989. Comparative study of vocal communication in two Asian leaf monkeys, *Presbytis johnii* and *Presbytis entellus*. *Folia Primatologica* 52: 27-57.
- Hohmann G. 1990. Loud calls of male purple-faced langurs (*Presbytis senex*). *Folia Primatologica* 55: 200-206.
- Horwich RH. 1976. The whooping display in Nilgiri langurs: an example of the daily fluctuations super-imposed on a general trend. *Primates* 17: 419-431.
- Horwich RH, Gebhard K. 1983. Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. *Primates* 24(2): 290-296.
- Janik VM, Slater PJB. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour* 56: 829-838.
- Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour* 67: 125-139.
- Kojima S, Izumi A, Ceugniet M. 2003. Identification of vocalizers by pant hoots, pant grunts and screams in a chimpanzee. *Primates* 44(3): 225-230.
- Konrad R, Geissmann T. 2006. Vocal diversity and taxonomy of *Nomascus* in Cambodia. *International Journal of Primatology* 27(3): 713-745.
- Kummer H. 1970. Behavioral characters in primate taxonomy. In: Napier JR, Napier PH, eds. *Old World Monkeys: Evolution, Systematics and Behavior*. New York: Academic Press, 25-36.
- Langmore NE, Davies NB. 1997. Female dunnocks use vocalizations to compete for males. *Animal Behaviour* 53: 881-890.
- Langmore NE, Davies NB, Hatchwell IR. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. *Proceedings of the Royal Society, London B* 263: 141-146.
- MacKinnon J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour* 22: 3-74.
- Manley GH. 1978. 'Wanderers' in *Presbytis senex*. In: Chivers DJ, Herbert J, eds. *Recent Advances in Primatology, Volume 1; Behaviour*. London: Academic Press, 193-195.
- Manley GH. 1986. Through the territorial barrier: harem accretion in *Presbytis senex*. In: Else JG, Lee PC, eds. *Primate Ontogeny, Cognition and Social Behaviours*. Cambridge: Cambridge University Press, 363-370.
- Marler P. 1972. Vocalizations of East-African monkeys. II. Black and white colobus. *Behaviour* 42: 175-197.
- Mittermeier RA, Valladares-Pádua C, Rylands AB, Eudey AA, Butynski TM, Ganzhorn JU, Kormos R, Aguiar JM, Walker S. 2006. Primates in peril: The world's most

- endangered primates, 2004-2006. *Primate Conservation* 20: 1-28.
- Nekaris KAI, de Silva Wijeyeratne G. 2008. *The Primates of Sri Lanka*. Colombo, Sri Lanka: Jetwing Hotels and Jetwing Eco Holidays under the Jetwing Research Initiative.
- Nietsch A. 1999. Duet vocalizations among different populations of Sulawesi tarsiers. *International Journal of Primatology* 20(4): 567-583.
- Nijman V. 2001. Effects of behavioural changes due to habitat disturbance on density estimation of rain forest vertebrates, as illustrated by gibbons (Primates: Hylobatidae). In: Hillegers PJM, de Iongh HH, eds. *The Balance Between Biodiversity Conservation and Sustainable Use of Tropical Rain Forests*. Wageningen: Tropenbos, 217-225.
- Nottenbohm F. 1972. The origins of vocal learning. *The American Naturalist* 106(947): 116-140.
- Oates JF, Trocco TF. 1983. Taxonomy and phylogeny of black-and-white colobus monkeys. *Folia Primatologica* 40: 83-113.
- Parker L, Nijman V, Nekaris KAI. 2008. When there is no forest left: fragmentation, local extinction, and small population sizes in the Sri Lankan western purple-faced langur (*Trachypithecus vetulus nestor*) in Southwestern Sri Lanka. *Endangered species research*, in press.
- Penteriani V. 2003. Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. *Ibis* [online] 145: E127-E135.
- Poirier FE. 1970. The communication matrix of the Nilgiri langur (*Presbytis johnii*) of South India. *Folia Primatologica* 13: 92-136.
- Ripley S. 1967. Intertroop encounters among Ceylon gray langurs (*Presbytis entellus*). In: Altmann SA, ed. *Social Communication Among Primates*. Chicago: The University of Chicago Press, 237-254.
- Ross MD, Geissmann T. 2007. Call diversity of wild male orangutans: a phylogenetic approach. *American Journal of Primatology* 69: 305-324.
- Rudran R. 2007. A survey of Sri Lanka's Endangered and endemic Western purple-faced langur (*Trachypithecus vetulus nestor*). *Primate Conservation* 22: 133-139.
- Shutler D, Weatherhead PJ. 1990. Targets of sexual selection: song and plumage of wood warblers. *Evolution* 44: 1967-1977.
- Steenbeek R, Assink P. 1998. Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). *Folia Primatologica* 69: 77-80.
- Struhsaker TT. 1967. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: Altmann SA, ed. *Social Communication Among Primates*. Chicago: University of Chicago Press, 281-324.
- Struhsaker TT. 1970. Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys. In: Napier JR, Napier PH, eds. *Old World Monkeys: Evolution, Systematics, and Behavior*. New York: Academic Press, 365-444.
- Temeles EJ. 1990. Interspecific territoriality of Northern harriers: the role of kleptoparasitism. *Animal Behaviour* 40: 361-366.
- Vogel C. 1973. Acoustical communication among free-ranging common Indian langurs (*Presbytis entellus*) in two different habitats of North India. *American Journal of Physical Anthropology* 38: 469-480.
- Waser PM, Brown CH. 1986. Habitat acoustics and primate communication. *American Journal of Primatology* 10: 135-154.
- Waser PM, Waser MS. 1977. Experimental studies of primate vocalizations: specializations for long-distance propagation. *Zeitschrift für Tierpsychologie* 43: 239-263.
- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3: 69-94.
- Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. In: Kroodsma DE, Millers EH, eds. *Acoustic Communication in Birds, Vol. 1*. New York: Academic Press, 131-181.
- Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location or rank for wild chimpanzees? *Animal Behaviour* 61: 1203-1206.
- Zar JH. 1999. *Biostatistical Analysis*. New Jersey: Prentice Hall.
- Zimmermann E, Vorobieva E, Wrogemann D, Hafen T. 2000. Use of vocal fingerprinting for specific discrimination of grey (*Microcebus murinus*) and rufous mouse lemurs (*Microcebus rufus*). *International Journal of Primatology* 21(5): 837-852.
- Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour* 53: 589-604.

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