

Wind suppresses calling in northern buff-cheeked crested gibbons (*Nomascus annamensis*)

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Abstract

Communication is multimodal, occurring through many different mediums, and enables relationships to be formed and regulated. As communication is costly to an individual, selection pressures have driven signal formats towards those that maximise the likelihood of success while still being affordable to those producing them. In vocal communication, the acoustic structures of calls and the associated behaviours ensure maximum transmission in an individual's environment, increasing the likelihood that the signal will reach the intended receiver. *Nomascus annamensis* (northern buff-cheeked crested gibbon), like other gibbon species, is inconspicuous and, as a result, vocalisation surveys are the best way to assess population size and density. I used data produced from vocalisation surveys of three populations of *N. annamensis* in Mondulkiri Province, Cambodia, to assess if wind speed, cloud cover, fog and rain the night before and the morning of surveys impacted calling probability. The findings suggest that wind speed and cloud cover significantly affect calling probability of *N. annamensis*. These findings are relevant for improving the accuracy of population estimates developed from vocalisation surveys.

Keywords

gibbons, communication, wind, calling probability, vocalisation survey

Introduction

Communication is extremely important as it enables the creation and regulation of relationships that are essential to the fitness and survival of individuals (Salmi et al. 2013). For primates inhabiting forest environments, vocal signals are the most efficient way of communicating over long distances, as visual and olfactory cues are likely to be obscured (Waser and Waser 1977; Salmi et al. 2013). Predation, habitat and social structure have shaped the vocal repertoire of primate species. For example, Gustison et al. (2012) found a positive correlation between social complexity and the size of a species' vocal repertoire. Vocalisations may function to alert group members to the presence of predators, maintain spatial orientation and advertise resource (mate/territory) holding ability (Cowlshaw 1996; Sun et al. 2011).

The transmission of acoustic signals is dependent on factors such as the frequency of the sound, the height from which the sound is produced, meteorological conditions and time of day (Waser and Waser 1977; Waser and Brown 1986; Bezerra et al. 2012). The production of vocalisations is energetically costly and can alert predators to the caller's location. As a result, selection pressures have acted on both the acoustic structures of vocalisations and the associated behaviours, driving them towards optimal transmission at minimum cost (Range and Fischer 2004). Range and Fischer (2004) found that the acoustic elements of vocalisations by *Cercocebus atys* (sooty mangabey) have evolved to minimise distortion while travelling through a forest environment. These acoustic adaptations are particularly important for long-distance calls, which are thought to have species dependent, intragroup and intergroup functions (Oliveira and Ades 2004). Intragroup functions of long calls include spatial coordination and alarm calling, while extragroup functions include mate and/or resource protection and mate acquisition (Oliveira and Ades 2004). Most primate long-distance calls have high amplitudes and low frequencies to minimise attenuation due to atmospheric absorption, scattering and interference from reverberations off the ground (Mitani and Stuht 1998; Oliveira and Ades 2004).

The calling behaviour of animals also reflects selection for optimal message transmission at minimal energetic cost. Mated pairs of *Aptenodytes patagonicus* (king penguins) take it in turns to hunt and to incubate their offspring (Lengagne et al. 1999). *Aptenodytes patagonicus* live in colonies composed of several thousand, on sub-Antarctic islands that experience strong winds (Lengagne et al. 1999). The penguins use vocalisations to locate each other on their return from the sea (Lengagne et al. 1999). Lengagne et al. (1999)

found that the number of calls produced increased with wind speed. Since background noise increases with wind speed, Lengagne et al. (1999) suggests that by increasing the number of calls the penguins are able to increase the probability of their signal reaching the receiver during a window of low-wind speed.

Many animals avoid signal interference by producing vocalisations during a 'sound window' where there is limited interference from ambient noise (Waser and Waser 1977). In a large portion of African savannas, near-surface atmospheric conditions are optimum for sound transmission at dusk and dawn (Larom et al. 1997). These optimal atmospheric conditions may have acted as a selection pressure on the calling behaviour of *Panthera leo* (lions): Schaller (1972) reported peaks in the number of calls at dusk and dawn. Waser and Waser (1977) studied the long-distance vocalisation of four Old World monkey species living in the Kibale forest: 1) *Lophocebus ugandae* (grey checked mangabey); 2) *Cercopithecus mitis* (blue monkey); 3) *Cercopithecus ascanius* (red-tailed monkey); and 4) *Colobus guereza* (black-and-white colobus). They found that the male long-range calls of *L. ugandae* were produced between 7–9 am, and those of *C. mitis* and *C. ascanius* in the first few hours after dawn, while the calls of *C. guereza* were all produced before dawn at around 5 am (Waser and Waser 1977). By calling in this early morning 'sound window', and using a low frequency, primates living in the forest environments are able to improve communication and reduce the cost of calling (Morrill et al. 2013).

Gibbons are the smallest of the apes and belong to the family Hylobatidae (Mootnick and Fan 2011). They typically live in territorial, socially monogamous family groups consisting of a male–female pair and their offspring (Sun et al. 2011). All gibbon species produce long-distance calls, known as songs, usually in the early morning (Geissmann and Nijman 2006; Sun et al. 2011). The contributions of the male and female in a pair are sex-specific and the song types of mate pairs differ between species (Geissmann and Nijman 2006; Sun et al. 2011). Duets are produced by 10 species (all belonging to the genera *Hoolock*, *Nomascus* and *Symphalangus*), duets and male solo songs are produced by four species (*Hylobates agilis*, *H. lar*, *H. muelleri* and *H. pileatus*), and female and male solo songs are produced by two species (*H. klossii* and *H. moloch*; Geissmann and Nijman 2006). The calls of gibbons are thought to have several functions, including spacing among groups, defence of resources, mate attraction and strengthening or advertising pair bond (Geissmann and Nijman 2006). The duets of crested gibbons (*Nomascus* spp.) are highly stereotyped and male-dominated with a high level of sexual specificity in their songs (Konrad and Geissmann 2006).

Nomascus annamensis is found east of the Mekong River in northeastern Cambodia, southern Vietnam and possibly southern Laos (Rawson et al. 2009). They primarily inhabit evergreen forests but are also found in semi-evergreen, mixed deciduous and bamboo forests (Rawson et al. 2009). Home ranges of *N. annamensis* are approximately 30 hectare, which is similar to other species of gibbon (Rawson et al. 2009). The diet of *N. annamensis* consists of fruit, leaves and flowers (Traeholt et al. 2006; Rawson et al. 2009). Gibbons are typically inconspicuous and are often hard to find because of their low visibility and unpredictable behaviour in response to humans (Rawson 2004). For this reason, under ideal conditions the long-range duets of gibbons can be heard from up to 3 kilometres away (Rawson 2004), and can be used to locate groups and conduct population surveys.

The aim of this study is to investigate if weather conditions affect calling probability in three populations of *N. annamensis*. This knowledge will help to improve the accuracy of population size and density estimates produced from vocalisation surveys. By using data sets from Rawson (2004) and Rawson et al. (2009) I will assess if rain the night before surveys, rain on the morning of surveys, wind, the presence of cloud or fog affected the likelihood of calling by *N. annamensis*. I predict that wind, which increases ambient noise and prevents the vocal signals from reaching the intended receivers, will reduce calling probability. I also predict that morning rain will decrease calling probability due to raindrops creating increased ambient noise. I will investigate the interaction of wind speed and cloud cover and predict that the effect of the combined presence of these weather conditions will result in decreased calling probability. The findings of my study will help build on those established in Rawson (2004) and assist in more accurately assessing the presence of gibbons and estimating population density.

Methods

Data sets

Data were collected from Rawson (2004) and Rawson et al. (2009), who conducted vocalisation surveys of three populations of *N. annamensis*, collecting a total of 115 samples. Data were collected at three different sites and calls were recorded from a total of 19 groups: three groups at Camp 6 and eight groups each at Elephant Rock and Snake Hill (Rawson 2004; Rawson et al. 2009).

Study sites

The data used in Rawson (2004) were collected at a study area in Mondulkiri Province, eastern Cambodia, referred to as Camp 6 (C6 in Figure 1). The forest is mixed deciduous and dry deciduous forest with seasonal meadows and is part of a logging concession area (Rawson 2004). The majority of the rainfall at Camp 6 occurs between May and October (Rawson 2004), in line with the wet season in Cambodia. Rawson et al. (2009) further used data collected in the Seima Biodiversity Conservation Area, which is also located in Mondulkiri Province (Figure 1). Vocalisation surveys were conducted in two nonoverlapping plots referred to as Elephant Rock and Snake Hill (ER and SH in Figure 1).

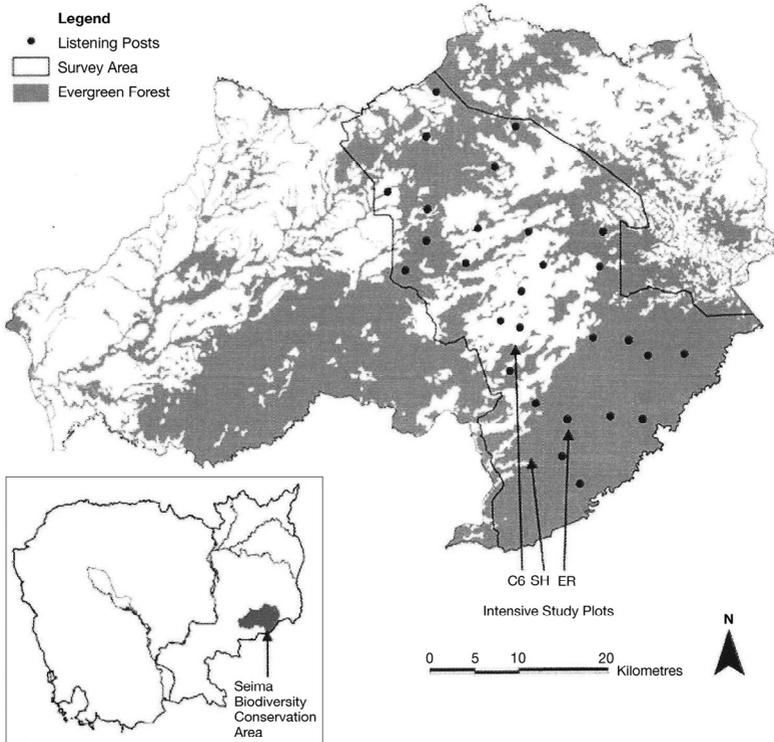


Figure 1: Map of study site locations

Source: Rawson et al. (2009).

Data collection

Vocalisation surveys at Camp 6 were conducted for at least five consecutive days per month for 11 months (December 2002 through October 2003) totalling 89 days (Rawson 2004). Surveys were conducted from 30 minutes before sunrise until 7 am from the fixed listening post (Rawson 2004). Duets and solo calls were recorded, as well as vocalisation start times, time of sunrise, duration of call and weather conditions (Rawson 2004). Data were collected at Elephant Rock and Snake Hill in December 2003 and January 2004, to coincide with the driest part of the year (Rawson et al. 2009). At each site, vocal surveys were conducted by the same individual over a total of 27 days: 13 consecutive days in December and 14 consecutive days in January (Rawson et al. 2009). All duet and solo calls heard between a half hour before sunrise and 12 pm were recorded, along with time of call, compass bearing of group, estimated distance and weather conditions (Rawson et al. 2009). In both studies, if a group stopped vocalising for more than five minutes before starting again it was considered a new 'bout' and analysed separately (Rawson 2004; Rawson et al. 2009). Cloud cover, wind and fog were recorded using a subjective scale of 0–3 (0=absent, 1=low, 2=medium, 3=high: Rawson 2004; Rawson et al. 2009).

Analysis

In order to increase the statistical power of my results, I combined the data collected from the three sites. As the number of *N. annamensis* groups at each site was known, I was able to conduct my analysis using the proportion of groups that called each day. I used a generalised linear model to assess the impact of wind, cloud, fog, rain and rain the night before on the calling probability of the combined study populations. As the data from Elephant Rock and Snake Hill were collected in the dry season there was no rain, and for this reason I assessed the impact of rain only the night before and morning of vocalisation surveys for Camp 6. I also considered the combination of the presence of wind and cloud for all locations. I adjusted the scale used by Rawson (2004) for cloud cover and wind, combining 'low' and 'medium' into a 'low' category, leaving me with three categories (absent, low and high).

Results

The presence of wind had a significant effect on mean calling probability ($\chi^2 = 7.014$, $df = 2$, $p = 0.03$), which decreased as a function of wind speed (Figure 2).

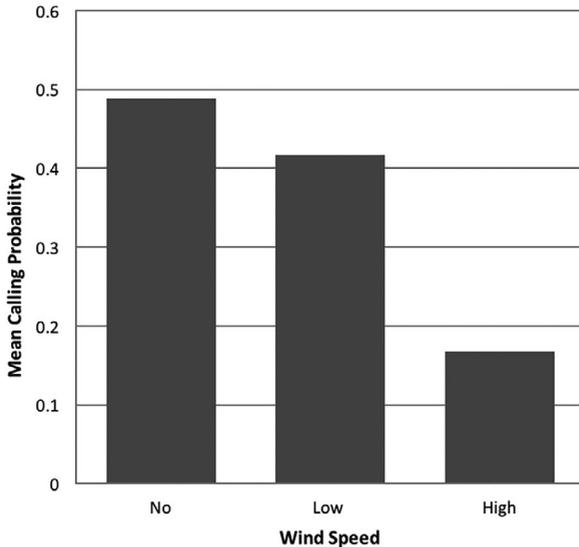


Figure 2: The effect of wind speed on mean calling probability

Source: Author.

The amount of cloud cover present had a significant effect on mean calling probability ($\chi^2 = 6.020$, $df = 2$, $p = 0.049$), with the probability of calling being lower when cloud cover was moderate or heavy compared to when cloud was absent (Figure 3). Mean calling probability increased slightly when cloud cover went from moderate to high (Figure 3).

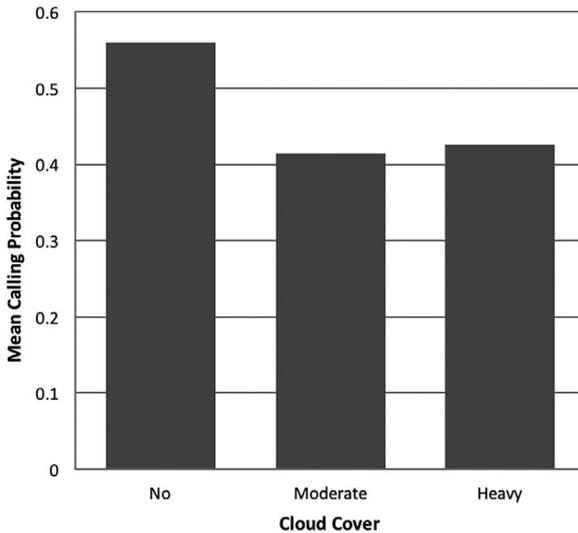


Figure 3: The effect of cloud cover on mean calling probability

Source: Author.

Fog was only present on 26.1 per cent of the days data were collected (30 of 115 total days), and did not have a significant effect on the mean calling probability of the sample populations ($\chi^2 = 0.922$, $df = 1$, $p = 0.337$). On days when fog was absent, the mean calling probability was 0.480, and on days where fog was present mean calling probability was 0.481.

When the impact of wind speed and cloud cover on calling likelihood were analysed together, the interaction was found to have a significant effect on mean calling probability ($\chi^2 = 4.059$, $df = 1$, $p = 0.044$; Figure 4). When wind speed was low, the probability of calling decreased between moderate to heavy cloud cover (0.453 and 0.344, respectively) (Figure 5). When wind speed was high, the probability of calling increased dramatically between moderate to heavy cloud cover (0.125 to 0.25, respectively) (Figure 6).

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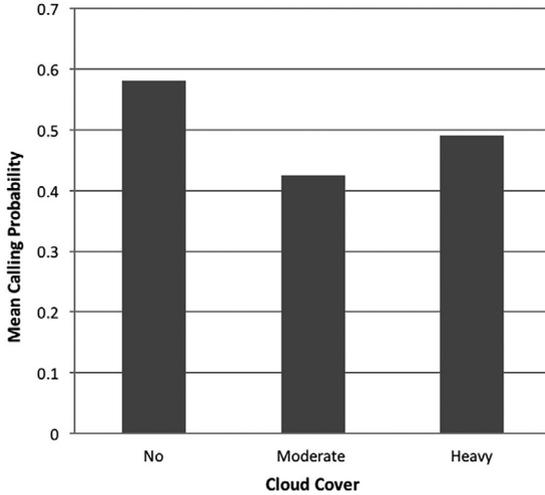


Figure 4: The effect of cloud cover when there is no wind on mean calling probability

Source: Author.

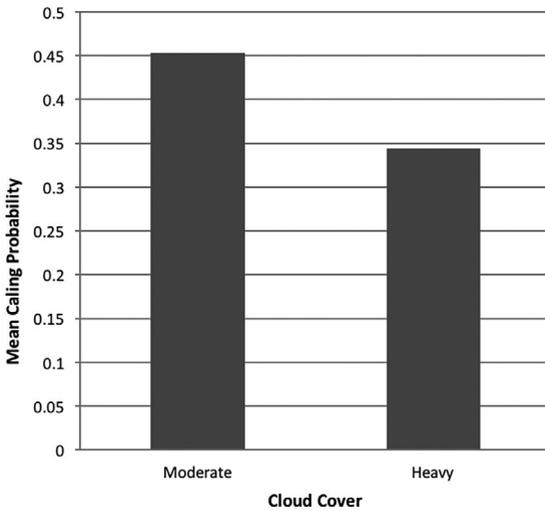


Figure 5: The effect of the interaction of low wind speeds and cloud cover on mean calling probability

Source: Author.

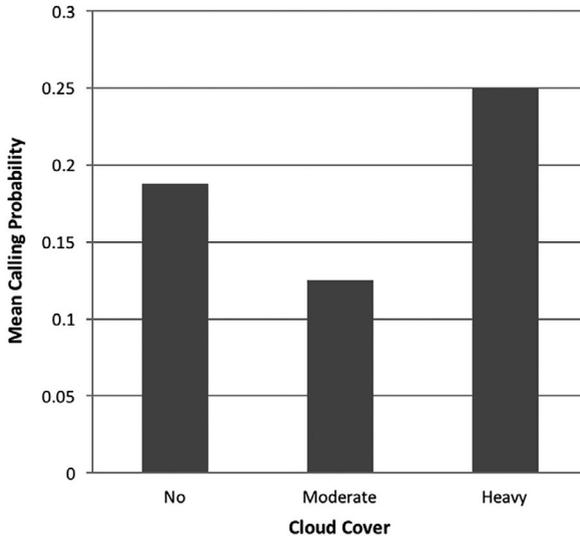


Figure 6: The effect of the interaction of high wind speeds and cloud cover on mean calling probability

Source: Author.

The effect of rain during the morning of surveys and the night before surveys was analysed only for Camp 6 data as there was no rain during the data collection periods at Elephant Rock and Snake Hill. Calls were heard on a total of 65 out of 89 survey days at Camp 6. Neither rain nor rain the night before had any significant effect on the calling probability.

Discussion

The results suggest that wind speed and the presence of cloud cover have an impact on the calling probability of *N. annamensis*. Wind speed had the largest effect on calling probability, which decreased as wind speed increased. Ambient noise, which prevents the clear transmission of vocal signals, increases with wind speed (Lengagne et al. 1999). The observed decrease in calling probability with increased wind speed may be a reflection of the gibbons being unable to communicate effectively when ambient noise reaches a certain level. If one of the main functions of the gibbon song is to transfer information to neighbouring groups, it is not energetically wise to participate in the costly behaviour if transmission conditions are not optimal (Haimoff 1984;

Geissmann and Nijman 2006; Cheyne et al. 2007). Wind is known to suppress calling, and a negative correlation between wind speed and calling frequency has been observed in many gibbon species (Brockelman and Ali 1987; Lengagne et al. 1999). It is interesting that the rainfall was not found to significantly impact calling probability, despite rain increasing ambient noise (Lengagne and Slater 2002). Both Hoang et al. (2010) and Rawson (2004) noted that *N. annamensis* were less likely to call on mornings when it rained, or during the wet season. The noise created by falling rain overlaps with the acoustic signals used by birds (Lengagne and Slater 2002); this is a higher frequency than that used by larger primates and may have contributed to rain having no effect on calling probability. It is more likely, however, that the results reflect small sample size as data collection at Elephant Rock and Snake Hill took place only during the dry season.

While cloud cover significantly impacted calling probability, this relationship was not as strong as that between calling probability and wind speed. Due to a lack of literature on the effect of cloud cover on acoustic signals, it is unclear how these results align with calling probabilities in other species. Cloud cover during the day reduces the temperature (Karl et al. 1993), and I suggest that the observed link between morning cloud cover and calling probability may have been caused by temperature variation. When the temperature is cooler, gibbons are required to allocate more energy to thermoregulation, reducing the energy available for behaviours such as calling (Fan et al. 2008). Further investigation into the relationship between temperature and the calling probability of *N. annamensis* is necessary to understand which variable is the cause of the observed variation in calling probability.

The interaction of wind and cloud significantly affected calling probability as predicted, particularly when the wind speed was high. While the presence of cloud cover was found to significantly impact calling probability, I was unable to separate the effects of cloud cover and temperature. It is also therefore unclear whether the observed variation in calling probability was a response to the combined effect of wind speed and cloud, or wind speed and temperature. Regardless, wind speed played the largest role in reducing the calling probability in this interaction.

Rain the night before and the presence of fog during vocalisation surveys had no effect on calling probability. Neither of these variables would interfere with the transmission of the gibbons' morning calls, as they do not create ambient noise during the singing period. The presence of cloud overnight and of morning fog prevents some of the previous day's heat from escaping, maintaining

warmer temperatures (Karl et al. 1993; Johnstone and Dawson 2010). While this should reduce the energetic cost of thermoregulation, my results suggest that the energy saved is not enough to have an impact on the likelihood of individuals calling.

Conclusion

In this study, I assessed the impact of wind speed, cloud cover, fog and rain the night before and during vocalisation surveys on the calling probability of *N. annamensis*. I found that wind speed had the most significant impact on calling probability as a result of increased ambient noise preventing the clear transmission of vocal signals. Cloud cover also significantly impacted calling probability, although further research needs to be done to separate the effects of cloud cover and temperature. As *N. annamensis*, like other gibbon species, is inconspicuous, vocalisation surveys are a particularly useful method of assessing populations. As seen in Rawson et al. (2009) and Hoang et al. (2010), vocalisation surveys of the species can be used to estimate population density. The more knowledge there is about the factors that influence calling likelihood, and the extent to which these factors suppress calling, the more accurate the estimates from vocalisation surveys will be.

Acknowledgements

I would like to thank Dr Alison Behie for her guidance in writing this essay and for facilitating my independent research topic. I would also thank Dr Ben Rawson for allowing me to use his data, Dr Teresa Neeman for assisting with my statistical analysis and the reviewers for their useful feedback.

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This text is taken from the *The Human Voyage: Undergraduate Research in Biological Anthropology: Volume 1, 2017*, edited by Alison Behie, published 2017 by ANU eView, The Australian National University, Canberra, Australia.

[dx.doi.org/10.22459/HV.01.2017.01](https://doi.org/10.22459/HV.01.2017.01)