Seasonal variation in the diet and activity budget of the northern yellow-cheeked crested gibbon *Nomascus annamensis*

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មូលន័យសង្ខេប

សត្វទោច (ព្លុក *Nomascus*) គឺជាក្រុមមួយ ក្នុងចំណោមក្រុមពានរផ្សេងៗទៀតដែលជិតផុតពូជ និង កង្វះការសិក្សានៅទូទាំងសាកល លោក។ សមាជិកមួយនៃក្រុមនេះគឺជាទោចថ្ពាល់លឿងនៅភូមិភាគត្បួងសាន *Nomascus annamensis* វាងការគម្រាមកំហែង និង ត្រូវបានលើកយកមកសិក្សាស្រាវជ្រាវខ្លះៗ។ ដោយការយល់ដឹងពីអាកប្បកិរិយានិងអេកូឡូស៊ីនៃប្រភេទ និង របៀបសម្របខ្លួនទៅ នឹងការផ្លាស់ប្តូរបរិស្ថានរបស់វា ជាការចាំបាច់សម្រាប់ការងារអភិរក្សនៃប្រភេទនេះ គោលបំណងរបស់យើងគឺដើម្បីកំណត់ពីរបៀប ដែល *N. annamensis* បន្ស៊ាំអាហារ និង អាកប្បកិរិយារបស់វាទៅនឹងការប្រែប្រួលនៃរដូវនៅភាគត្បួងសាននៃប្រទេសកម្ពុជា។ យើង បានប្រើប្រាស់វិធីសាស្ត្រប្រមូលទិន្នន័យតាមបែបបរហ័ស ដើម្បីកំណត់បរិមាណបែបអាហារ និង សកម្មភាពរស់នៅរបស់ទោចមួយក្រុម នៅខ្ស្យានជាតិវ៉ុនសៃ-សៀមប៉ាង ចាប់ពីឆ្នាំ២០០៧ ដល់ ២០១៩។ លទ្ធផលបង្ហាញថា សកម្មភាពរបស់វាគឺប្រែប្រួលទៅតាមរដូវ ដែលការប្រែប្រួលនេះទំនងជាបណ្ដាលមកពីសកម្មភាពស៊ីចំណីរបស់វា។ មានការកើនឡើងខ្លាំងនូវការស៊ីស្លឹកឈើ និង មានការធយ ចុះនូវការស៊ីផ្លែឈើក្នុងរដូវប្រាំង(វិច្ឆិកា-មេសា)។ ដោយការស៊ីស្លឹកឈើកើនឡើង សត្វទោចចំណាយពេលភាគច្រើនលើការស៊ីចំណី និងភាគតិចទៅលើសកម្មផ្សេងៗទៀត បើធៀបទៅនឹងរដូវវស្សា(ឧសភា-តុលា)។ ជារួម ទិន្នន័យរបស់យើងស្មើថា *N. annamensis* បង្ហាញពីទម្រង់អាកប្បកិរិយាស្រដៀងគ្នាទៅនឹងប្រភេទទោចផ្សេងៗទៀត ដែលត្រូវបានសិក្សាចងក្រង។

Abstract

Crested gibbons (genus *Nomascus*) are among the most highly endangered and understudied primates on the planet. One member of the group, the northern yellow-cheeked crested gibbon *Nomascus annamensis*, is similarly threatened and has been subject to few published studies. Because understanding the behaviour and ecology of a species and how it adjusts to changes in its environment are integral to its conservation, our aim was to determine how *N. annamensis* adapts its diet and behaviour to seasonal changes in northeastern Cambodia. To this end, we employed instantaneous scan sampling to quantify the diet and activity of a habituated group in Veun Sai-Siem Pang National Park from 2007 to 2014. Our results indicate that activity varied seasonally, and that this variation was likely due to changes in feeding activity. There was a pronounced increase in leaf consumption and a decrease in fruit consumption during the dry

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(November–April) season. With the increase in folivory, gibbons spent more time eating overall and less time on other activities compared to the wet season (May–October). Overall, our data suggests that *N. annamensis* exhibits behavioural patterns similar to other gibbon species.

Keywords

Activity budget, gibbon, Hylobatidae, *Nomascus*, seasonal diets.

Introduction

The pronounced seasonality of some tropical forests has a strong influence on the availability of food resources (Janson & Chapman, 1999; Corlett, 2014). Primates often respond to these seasonal changes in food availability through dietary and behavioural changes (e.g., Poulsen *et al*., 2001). Seasonal variation in the diets of most primates often results in changes to activity patterns as a result of having to balance energy intake with the metabolic costs of maintaining body condition and reproduction (Milton, 1980). Because this depends on food quality, habitat structure and factors intrinsic to a species however, there is no universal behavioural response to dealing with periods of food shortage. For example, capped langurs *Presbytis pileatus* spend more time foraging when fruit is scarce (Stanford, 1991), whereas black howler monkeys *Alouatta pigra* spend more time inactive during periods of fruit scarcity (Pavelka & Knopff, 2004). Judging from available information on the northern *Nomascus* gibbons (*N. nasutus* and *N. concolor*), it is apparent that these also vary their activity patterns seasonally in response to changes in fruit availability. When fruit consumption is low, these animals conserve energy by spending more time inactive and less time feeding (Fan *et al*., 2008). Because large frugivorous primates are most vulnerable following habitat disturbance due to changes in patterns of fruit production and availability (Johns & Skorupa, 1987), understanding how these animals interact with their environment and deal with such changes is important.

Few gibbon species have been subjected to long-term studies thus far, the most notable exception being the white-handed gibbon *Hylobates lar* (Reichard & Barelli, 2008; Reichard, 2009). This is true for crested gibbons (*Nomascus*), a diverse genus which comprises seven species distributed from southern Vietnam and eastern Cambodia to southwestern Cambodia. Only three *Nomascus* species have received detailed ecological studies to date: the black crested gibbon *N. concolor* (Fan & Jiang, 2008; Fan *et al*., 2009a,b), the Cao-vit gibbon *N. nasutus* (Fan *et al*., 2012a,b) and the southern yellow-cheeked crested gibbon *N. gabriellae* (Kenyon, 2007; Kenyon *et al*., 2010; Bach *et al*., 2017). Little is known

about the four remaining species beyond status reports and taxonomic descriptions (e.g., Traeholt *et al*., 2005; Duckworth, 2008; Rawson *et al*., 2011). We consequently present the first study of the behaviour and ecology of the northern yellow-cheeked crested gibbon *N. annamensis*, a recently described gibbon species occurring in northeastern Cambodia, southern Laos and east central Vietnam (Thinh *et al*., 2010b). Prior to its description (Thinh *et al*., 2010a), individuals within the distribution range of the species were assigned either to the more southerly *N. gabriellae* or the more northerly *N. siki*, although researchers had hypothesized that an additional and intermediately distributed taxon might exist based on vocalization analysis (Geissmann *et al*., 2000; Konrad & Geissmann, 2006). This was later confirmed by genetic and vocal characteristics (Thinh *et al*., 2010a,b).

Although the conservation status of *N. annamensis* has yet to be formally assessed, the species will likely qualify as Endangered on the IUCN Red List. Population surveys in Vietnam have revealed that as few as 200 groups have been recorded over the last decade with the largest known subpopulation comprising approximately 80 groups (Rawson *et al*., 2011). Populations of the species remain largely unknown in Laos, with none under effective protection, leaving those that exist extremely vulnerable to high levels of hunting pressure and habitat destruction (MAF, 2011). In Cambodia, the species occurs in the northeastern forests of Virachey National Park, Siem Pang Wildlife Sanctuary and Veun Sai-Siem Pang National Park, with the latter supporting an estimated 450 groups (Rawson, B. unpubl. data). While data on the overall population status of *N. annamensis* are relatively good, very little behavioural information exists for the species or for the more southerly *Nomascus* taxa in general, with the exception of two studies on *N. gabriellae* in southern Vietnam (Kenyon, 2007; Kenyon *et al*., 2010).

As a consequence, we present the activity budget and feeding ecology of a group of *N. annamensis* in northeastern Cambodia. The purpose of our study was to understand how the species adjusts its feeding and other behavioural activities over time and in response to seasonal change in an environment with relatively few threats. Because habitat destruction presents a major

threat to *N. annamensis*, our overall goal was to improve knowledge of how the species adjusts its behaviour due to seasonal changes in food availability to better predict how it might respond to habitat and climate change in future.

Methods

Study site and study group

Data were collected between November 2007 and April 2013 in the Veun Sai–Siem Pang National Park (formerly a Conservation Area) (VSSP; 14°01′N, 106°44′E), a predominantly low elevation region (ca. 100 m) in northeastern Cambodia. The national park (56,000 ha) forms part of the Indo-Burmese forest biodiversity hotspot (Myers *et al*., 2000) and mostly comprises semi-evergreen and evergreen tropical forest. The wet season usually begins in April or May and continues until October. From 2008 to 2012, mean annual rainfall was 1,919 mm and averaged 400 mm per month during the wet season which usually peaked around August. The dry season runs from November to April with an average of 3 mm of rain per month and the driest month is December (Schneider *et al*., 2011).

Four hundred and fifty groups of *N. annamensis* are estimated to occur in VSSP, which is the largest documented population of the species (Rawson, B. unpubl. data). While hunting with guns is a major threat to the species in Vietnam and Laos (MAF, 2011; Rawson *et al*., 2011), guns have yet to become prevalent at VSSP where hunters mainly use dogs and crossbows. Because arboreal primates are less vulnerable to the latter (Iseborn, 2011), this could be one reason for the large population of *N. annamensis* in VSSP.

A single group of gibbons was followed for the purposes of our study. This group was first habituated for a two-month period and subsequently studied for two years (2005–2007) by a team led by Fauna & Flora International (Traeholt *et al*., 2007). Although the group was still wary and often lost after a few hours of contact in the early years of our study, it became comfortable with the presence of observers by 2011. So much so, that the adult male frequently descended almost to the ground on numerous occasions. The group consisted of an adult male and an adult female, and two immature individuals, the younger of which was likely born in 2007. A third infant was born in August 2011 but disappeared in March 2012. Gibbons generally live in small family groups, usually a socially monogamous pair and their offspring (Brockelman, 2009), although there are

plenty of exceptions, including *N. concolor* for which polygynous groups are common (Fan & Jiang, 2010).

Behavioural data collection

We documented gibbon activity through instantaneous group-scan sampling, where the behaviour of visible individuals was documented at ten-minute intervals during contact time with the group. Gibbons were located in the morning by their song and followed until lost or when they settled in their sleeping tree for the night. Following the gibbons was quite difficult, particularly in the first few years of the study when they were less habituated and the group was frequently lost by midday. Because approximately 76% of our observational data was generated between 05:00–11:00 hrs, we acknowledge the potential existence of an information gap and consequently pooled data where appropriate to reduce possible bias.

Activities (and their sub-categories) were classified as: *social* (singing, playing, grooming, copulation and agonistic), *inactive* (scanning or resting), *feeding* (food type recorded), *travel* (brachiate, jumping, dropping, walking bipedally, walking quadrupedally and climbing), *other behaviour* or *out of view*. We tagged and recorded the locations of all plants used by the gibbons for sleeping, eating and singing, and these were subsequently identified by local researchers. Canopy use by each gibbon observed during the instantaneous scans was categorized as: low (<5 m), middle (5–15 m) or high (>15 m). The location of each scan was also recorded using GPS units and plotted in Google Earth to estimate the total range of the group over the course of the study period.

Data analysis

We used Spearman rank correlations of plant part consumption and activity categories to assess relationships between diet and activity patterns. SPSS vers. 20.0 was employed for these tests with a (two-tailed) statistical significance value of $p<0.05$. Precipitation data were acquired from the GPCC Global Precipitation Climatology Centre (Schneider *et al*., 2011). To examine relationships between precipitation, activity and diet, monthly data were aggregated by year to determine the effect of precipitation on the probability of a gibbon being documented as traveling, feeding and eating different plant parts. Analysis was undertaken using R vers. 3.0.2 (R Core Team, Austria) using generalized maximum likelihood with a logit link. As data were not normally distributed, Mann-Whitney U tests were employed for sex-based comparisons (male n=50, female n=50). Because the sex of juvenile *N. annamensis* cannot be

confirmed visually, only data from adults were used for sex-based comparisons of diet and activity.

Results

Activity budgets

A total of 1,368 hours of contact time were spent with the study group from 2007 to 2013, resulting in 32,040 scans. Overall, inactivity accounted for most of the group's daily activity budget at 31.8%, followed closely by travel (30.3%) and feeding behaviour (26.3%). The remaining time was spent in social interactions (10.4%) and other behaviour (1.3%). For time spent on travel, 43.7% was spent brachiating, 24.6% was spent jumping and 17.1% was spent dropping. The remainder was devoted to walking, either bipedally (7.5%) or quadrupedally (4.8%), and climbing (2.0%). Time spent socializing was largely spent playing (54.4%) and vocalizing (40.3%), with the remainder dedicated to grooming, copulating and agonistic. The observed range of the group during the study period was estimated at 1.27 km^2.

Social behaviour among the gibbons peaked in early morning (before 07:00 hrs; Fig. 1), which comprised singing of the dawn duet song. Travel and feeding behaviour peaked between 07:00 and 10:00 hrs and slowly tapered off as the afternoon progressed, with the animals becoming inactive by 16:00 hrs (Fig. 1). There was no seasonal variation in this pattern. Because days when the gibbons did not sing were inconsistently recorded, we were unable to quantitatively assess field observations (Frechette, J. pers. obs.) that the group avoided singing during rain.

The frequency of feeding behaviour was greater during the dry season (November–April) compared to the wet season (May–October; Fig. 2) and precipitation had a significant negative effect on the probability of feeding ($p=<0.001$; Fig. 3a). Logistic regression analysis showed that precipitation also had significant positive effect on the probability of traveling ($p=<0.001$; Fig. 3b) and inactivity ($p=<0.001$; Fig. 3c). No significant differences in activity were observed between males and females.

Diet and feeding behaviour

Fruit comprised over half of the study group's diet, constituting 58.6% of the total related scans (Fig. 4). We identified 56 different species of fruit consumed by gibbons. *Ficus* spp. was the most common fruit consumed, constituting ca. 14% of the total fruit diet, although the most commonly eaten fruit sometimes varied annually (Table 1). Young leaves formed the next highest proportion of the diet at 25.5%, while flowers comprised 10.6%. The most common species of flower eaten was *Dipterocarpus costatus*, which composed 60% of the observed flower diet (Table 2). Approximately 90% of all flowers
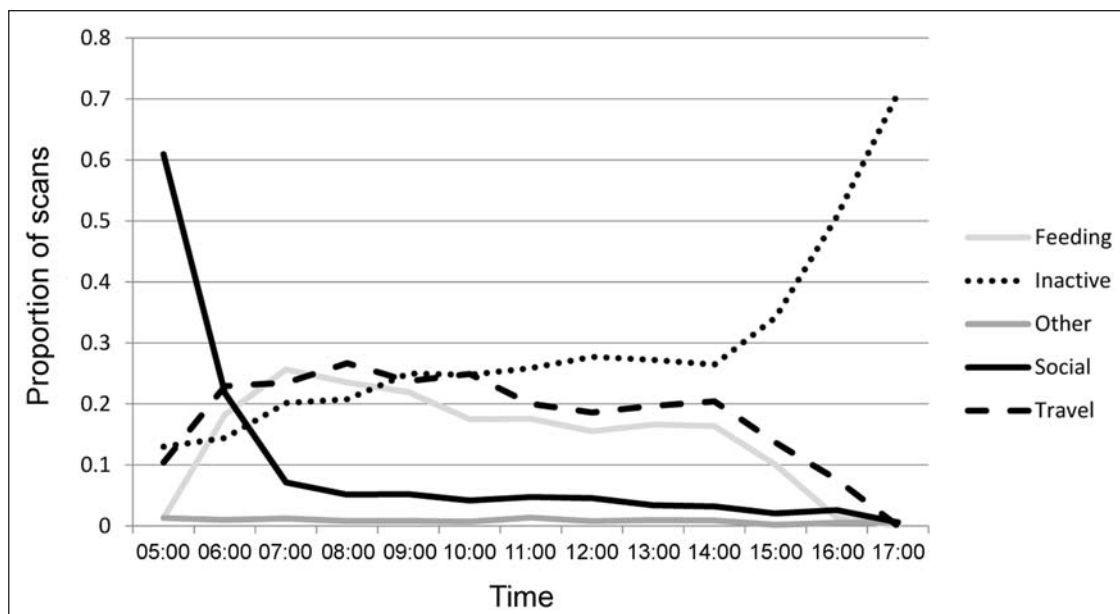

Fig. 1 Daily activity pattern of yellow-cheeked crested gibbons *N. annamensis in* Veun Sai–Siem Pang National Park, northeastern Cambodia, 2007–2013.
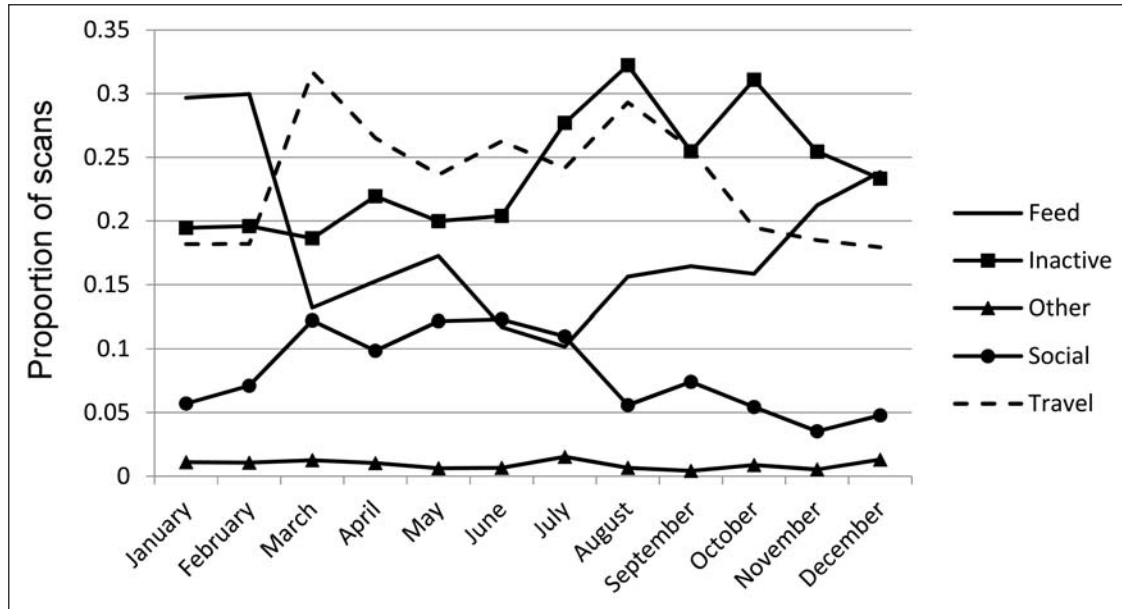
Fig. 2 Monthly variation in activity of yellow-cheeked crested gibbons *N. annamensis* in Veun Sai–Siem Pang National Park, northeastern Cambodia, 2007–2013.
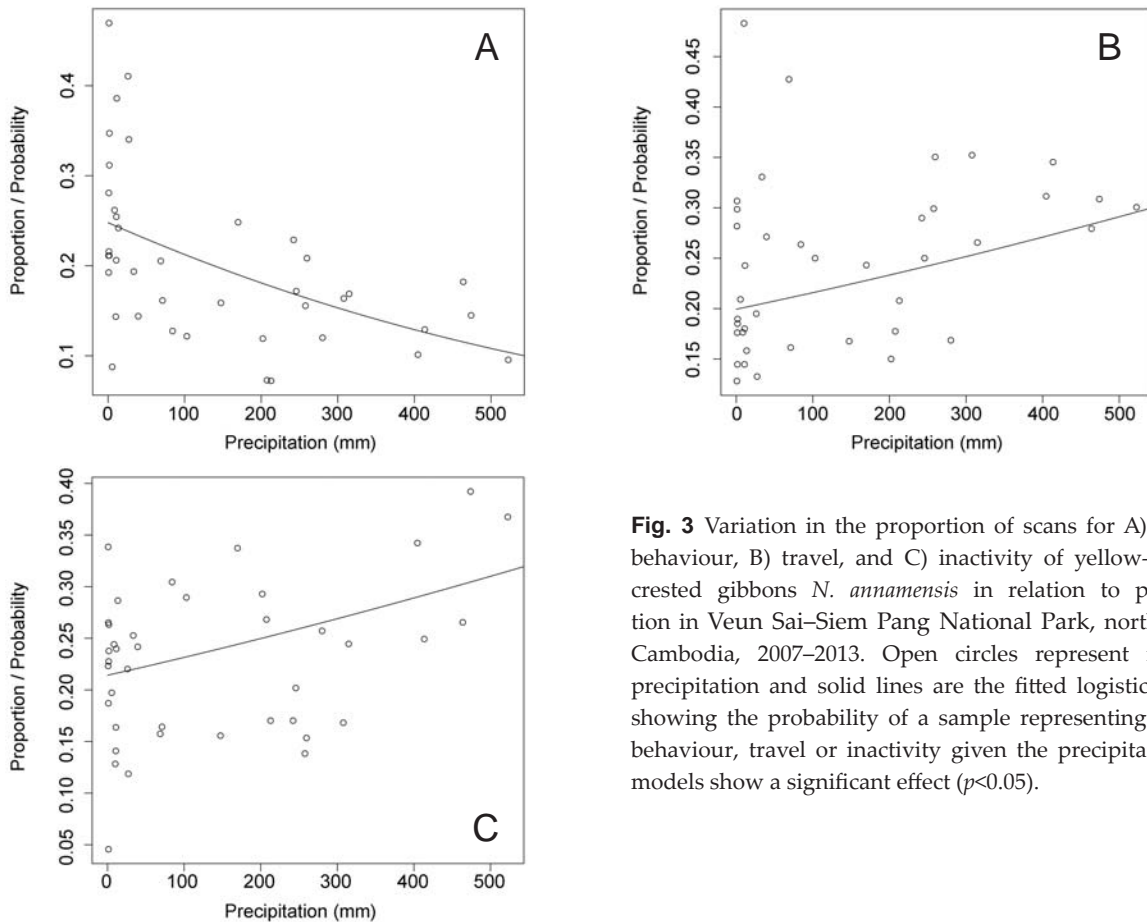

Fig. 3 Variation in the proportion of scans for A) feeding behaviour, B) travel, and C) inactivity of yellow-cheeked crested gibbons *N. annamensis* in relation to precipitation in Veun Sai–Siem Pang National Park, northeastern Cambodia, 2007–2013. Open circles represent monthly precipitation and solid lines are the fitted logistic models showing the probability of a sample representing feeding behaviour, travel or inactivity given the precipitation. All models show a significant effect ($p<0.05$).
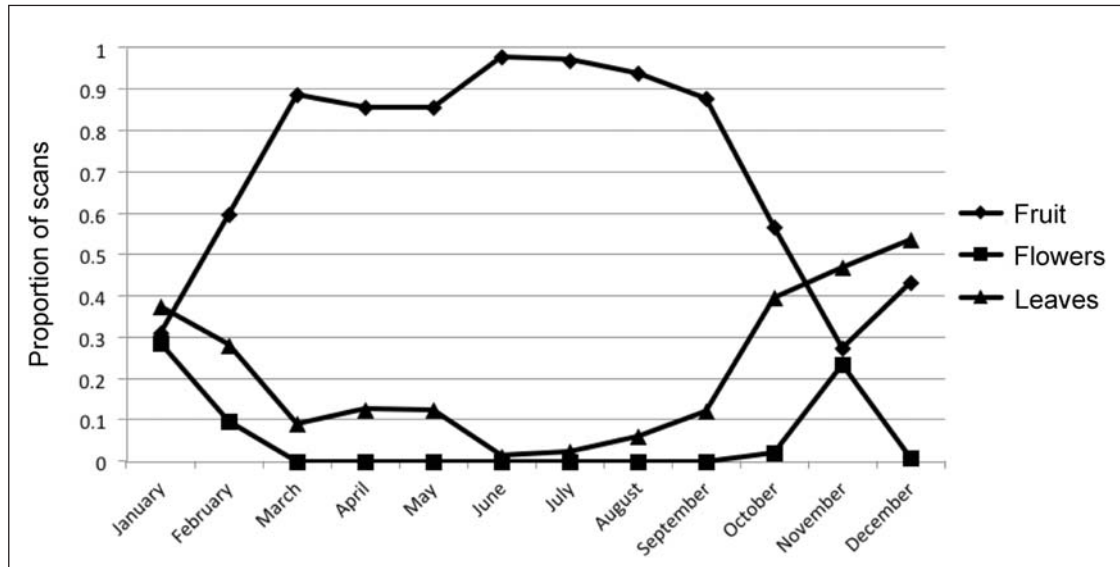
Fig. 4 Monthly variation in the proportions of scans that yellow-cheeked crested gibbons *N. annamensis* spent eating different plant parts in Veun Sai–Siem Pang National Park, northeastern Cambodia, 2007–2013.

eaten belonged to the Dipterocarpaceae (Table 2). The remaining portions of the diet comprised mature leaves (1.4%), leaves of unknown maturity (1.9%) and other items that could not be confidently identified (1.4%).

Fruit consumption peaked during the wet season (April–October), whereas leaf and flower consumption peaked during the dry season (Fig. 4). Logistic regression models indicated significant positive correlations between fruit consumption and precipitation (p=<0.001; Fig. 5a), whereas consumption of leaves (p=<0.001; Fig. 5b) and flowers (p=<0.001; Fig. 5c) were significantly negatively related to precipitation. The decrease in fruit consumption during the dry season was also significantly and negatively correlated with time spent feeding (r_{sp}=0.596; p=0.001), indicating that when fruit consumption decreases, animals spend more time feeding. There were no differences in food consumption between the sexes.

Canopy use

Our study group used the upper canopy (>15 m) most often (57.0%), followed by the middle canopy (5–15 m: 42.1%). Although the gibbons did use the lower canopy (<5 m) on occasion, <1% of behaviour occurred in this forest stratum. The amount of time spent in the lower canopy increased during the rainy season (Fig. 6), although insignificantly. The adult male also spent more time than the adult female in the lower canopy (2.69 vs. 0.66% respectively; z=2.015; p=0.04).

Discussion

Our study gibbons showed distinct seasonality in behavioural patterns in response to precipitation. The group was highly frugivorous but had a seasonal dependence on leaves and flowers. Dietary shifts coincided with changes in rainfall, which were likely indicative of fruit availability (see below). Overall, our data indicate that the activity and feeding patterns of *N. annamensis* are similar to those of other gibbon species. These include *Hoolock leuconedys* (Fan *et al.*, 2013), *Hylobates lar* (Raemaekers, 1978; Palombit, 1997), *N. gabriellae* (Bach *et al.*, 2017), *N. nasutus* (Fan *et al.*, 2012a), *N. concolor* (Fan *et al.*, 2008) and *Symphalangus syndactylus* (Chivers, 1974; Palombit, 1997).

Our study group mostly began singing between 05:00 and 07:00 hrs and rarely sang more than once a day. Because the adult male and female sang together in a duet, this resulted in social behaviour peaking in early morning and juveniles occasionally joined in singing bouts. This is consistent with studies of *N. gabriellae* which found that 60% of calling bouts occurred during a 30 minute window that began 10 minutes before sunrise, with 80.6% of calls occurring in the first hour after dawn (Rawson, 2004; Kenyon, 2007). Rawson (2004) also found that single bouts of song were the norm for *N. gabriellae*, suggesting that its vocal behaviour is similar to *N. annamensis*. In our study, this peak in social behaviour was followed by a long period of traveling and feeding which peaked before 10:00 hrs and subsequently decreased until 14:00 hrs at which point it slightly increased before declining dramatically. This pattern of activity is similar

Table 1 Frequency and relative proportion of scans for each fruit species consumed by yellow-cheeked crested gibbons *N. annamensis* in Veun Sai–Siem Pang National Park, northeastern Cambodia. Figures in the sum proportion column equal the proportion of the total number of scans. Seeds eaten: Y=Yes, N=No, U=Unknown. *= <0.01.

Species	No. of scans	Proportion of scans							Sum proportion	Seeds eaten
		2007	2008	2009	2010	2011	2012	2013		
Unknown	838	0.43	0.13	0.14	0.35	0.22	0.24	0.04	0.2201	
Ficus sp. (Moraceae)	542	0.07	0.04	0.20	0.12	0.25	0.08	0.11	0.1423	Y
Willughbeia edulis (Apocynaceae)	423	-	0.05	*	0.09	0.15	0.08	0.41	0.1111	Y
Mircrocos paniculata (Malvaceae)	270	-	0.02	0.04	0.15	0.05	0.09	-	0.0709	Y
Nephelium hypoleucum (Sapindaceae)	260	0.07	0.04	0.08	0.08	*	0.14	-	0.0683	Y
Syzygium sp. (Myrtaceae)	206	-	0.06	-	0.01	0.07	0.08	-	0.0541	Y
Garcinia schomburgkiana (Clusiaceae)	196	-	0.15	-	0.07	0.02	0.07	-	0.0515	Y
Parinari annamensis (Chrysobalanaceae)	86	-	0.02	-	0.03	-	0.05	-	0.0226	N
Bouea oppositifolia (Anacardaiceae)	85	-	0.06	-	0.01	0.05	-	-	0.0223	Y
Dialium cochinchinensis (Fabaceae)	84	0.43	-	0.09	-	*	0.04	-	0.0221	Y
Anisoptera costata (Dipterocarpaceae)	72	-	0.14	-	-	0.01	-	-	0.0189	N
Dipterocarpus costatus (Dipterocarpaceae)	64	-	-	0.01	-	-	0.05	0.01	0.0168	N
Irvingia malayana (Irvingiaceae)	61	-	*	-	-	0.04	0.01	-	0.0160	N
Madhuca elliptica (Sapotaceae)	60	-	-	0.04	-	0.04	-	-	0.0158	Y
Colophyllum sp. (Calophyllaceae)	59	-	-	-	0.05	-	0.01	0.08	0.0155	Y
Vor Tnang (Local name)	56	-	0.12	0.01	-	-	*	0.01	0.0147	Y
Vor Antong (Local name)	48	-	-	-	*	-	0.04	-	0.0126	Y
Vor Sleng (Local name)	48	-	-	-	*	-	-	0.25	0.0126	Y
Khoh (Local name)	35	-	*	0.09	*	-	0.01	-	0.0092	Y
Mak Derk Kory (Local name)	26	-	-	0.09	-	-	-	-	0.0068	U
Khor Mouy (Local name)	25	-	-	0.08	*	-	-	-	0.0066	U
Sandoricum koetjape (Meliaceae)	23	-	0.05	*	-	-	-	-	0.0060	Y
Vor Tong (Local name)	23	-	0.05	-	-	-	-	-	0.0060	Y
Vor Krovanh (Local name)	21	-	-	0.01	-	0.01	-	-	0.0055	Y
Vor Tang Ant (Local name)	20	-	-	0.06	0.01	-	-	-	0.0053	Y
Yang Ying (Local name)	19	-	-	-	-	0.02	-	-	0.0050	U
Bok Nang (Local name)	17	-	-	-	-	*	-	0.06	0.0045	U
Sayak (Local name)	14	-	0.03	-	-	-	-	-	0.0037	U
Calamus palustris (Arecaceae)	13	-	-	-	0.02	-	-	-	0.0034	Y
Dong Kov Ankoy (Local name)	12	-	-	-	-	0.01	-	-	0.0032	U
Vor Khay Khov (Local name)	12	-	-	-	-	0.01	-	-	0.0032	U
Mak Takorng (Local name)	9	-	-	0.03	-	-	-	-	0.0024	Y
Kakoung (Local name)	8	-	-	-	-	0.01	-	-	0.0021	U
Pok Nang (Local name)	8	-	-	-	-	0.01	-	-	0.0021	U
Vor Chro Kor (Local name)	8	-	-	-	0.01	*	-	-	0.0021	U
Makuak (Local name)	6	-	-	-	-	-	-	0.03	0.0016	U
Vor Khay Kov (Local name)	6	-	-	-	-	0.01	-	-	0.0016	U
Euphoria cambodiana (Sapindaceae)	5	-	-	-	-	*	*	-	0.0013	Y
Anomianthus dulcis (Annonaceae)	5	-	0.01	-	-	-	-	-	0.0013	Y

Table 1 Continued

Species	No. of scans	Proportion of scans							Sum proportion	Seeds eaten
		2007	2008	2009	2010	2011	2012	2013		
Vor Takoung (Local name)	5	-	-	-	-	-	*	-	0.0013	U
Kleang (Local name)	4	-	-	-	-	*	-	-	0.0011	U
Mak Kong (Local name)	4	-	-	-	-	*	-	-	0.0011	U
Mouy (Local name)	4	-	-	-	-	*	-	-	0.0011	U
Mak Peng (Local name)	3	-	0.01	-	-	-	-	-	0.0008	U
Mitrella mesnyi (Sapindaceae)	3	-	-	0.01	-	-	-	-	0.0008	Y
Trobok (Local name)	3	-	-	-	-	*	-	-	0.0008	U
Fagraea fragrans (Gentianaceae)	2	-	-	-	-	*	-	-	0.0005	Y
Bok Yum (Local name)	1	-	-	-	-	-	*	-	0.0003	U
Brung Yum (Local name)	1	-	-	-	-	-	*	-	0.0003	U
Garcinia sp. (Clusiaceae)	1	-	-	-	-	*	-	-	0.0003	Y
Porki Pheng (Local name)	1	-	-	*	-	-	-	-	0.0003	U
Sro Tap (Local name)	1	-	-	-	-	-	*	-	0.0003	U
Vor Khay Khov (Local name)	1	-	-	-	-	*	-	-	0.0003	U
Xylopia vielana (Annonaceae)	1	-	-	-	-	-	*	-	0.0003	Y

Table 2 Frequency and relative proportion of scans for each flower species consumed by yellow-cheeked crested gibbon *N. annamensis* in Veun Sai–Siem Pang National Park, northeastern Cambodia.

Species	No. of feeding observations	Proportion of observations
Dipterocarpus costatus (Dipterocarpaceae)	410	0.606
Anisoptera costata (Diperterocapraceae)	201	0.297
Unknown species	45	0.066
Koh (local name)	12	0.018
Garcinia schomburgkiana (Cluseasaceae)	4	0.006
Hopea sp. (Dipterocarpaceae)	3	0.004
Sterculia lychnophora (Malvaceae)	2	0.003
Total	677	

to that reported for *N. concolor* and *H. agilis*, although these species have a more pronounced bimodal pattern of feeding behaviour which peaks in mid-afternoon (Gittens, 1982; Fan *et al.*, 2008).

Gibbons are considered highly frugivorous, but as we document here, frugivory is highly seasonal in *N. annamensis*. Figs (*Ficus* spp.) appear to be an important fruit item for the species, similar to other gibbon taxa (McConkey *et al.*, 2003; Fan *et al.*, 2009a). During the dry season, fruit consumption significantly decreased within our study group while leaf and flower consumption significantly increased. This likely reflects decreased fruit availability during the dry season, which is common for seasonal forests in Southeast Asia (Fan *et al.*, 2013; Corlett, 2014). We also found a strong negative relationship between fruit consumption and feeding time, indicating that when fruit availability declines during the dry season, *N. annamensis* compensates by devoting more time to feeding.
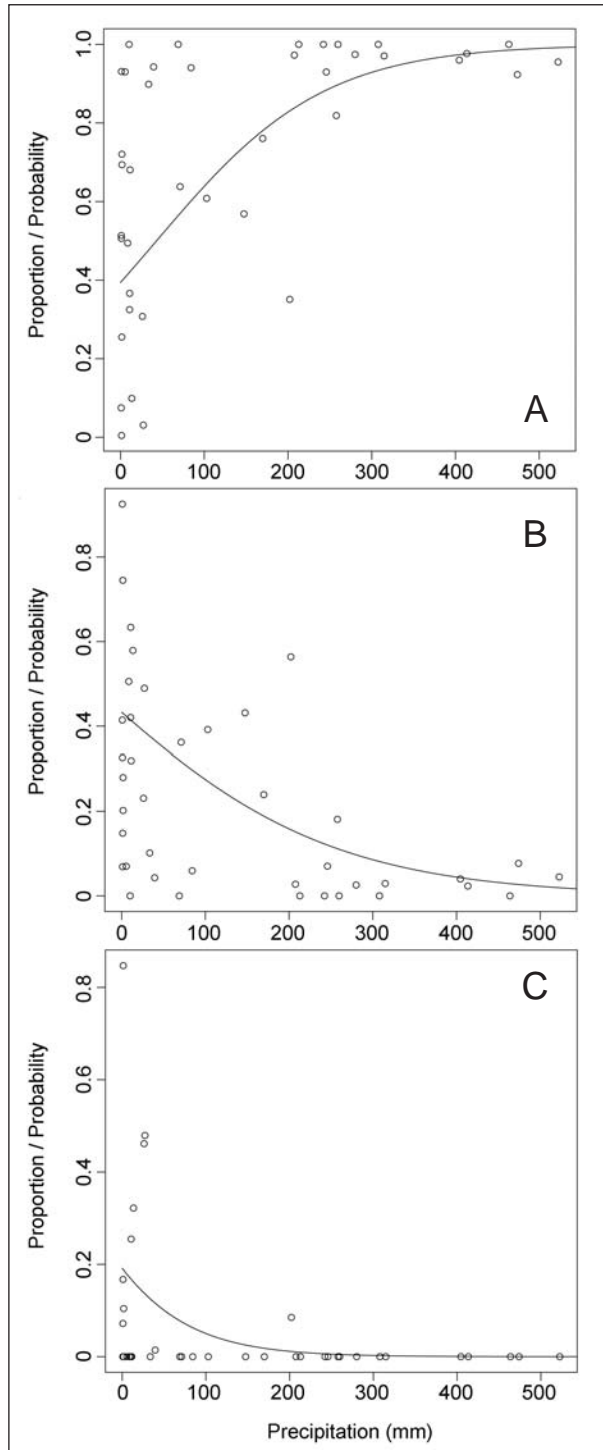
Fig. 5 Seasonal differences in diet as reflected in the proportion of scans for A) fruit, B) leaves, and C) flowers consumed by yellow-cheeked crested gibbons *N. annamensis* in Veun Sai–Siem Pang National Park, northeastern Cambodia. Open circles represent monthly precipitation and solid lines are the fitted logistic models showing the probability of a gibbon eating fruit, leaves or flowers in relation to precipitation. All models show a significant effect (*p*<0.05).
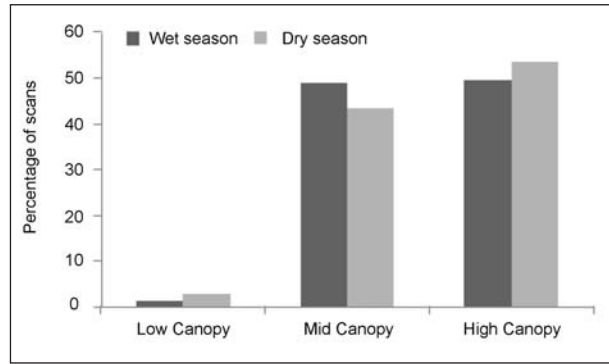

Fig. 6 Seasonal differences in canopy use by yellow-cheeked crested gibbons *N. annamensis* in Veun Sai–Siem Pang National Park, northeastern Cambodia.

Because leaves have a lower energy content than fruit (Hamilton & Galdikas, 1994), gibbons may need to spend more time eating the former to meet their energy demands when fruit is not available (Raemaekers, 1978; Fan *et al.*, 2008). However, recent studies of the highly frugivorous spider monkey *Ateles chamek* show that this species selects food items to maintain protein rather than energy intake, indicating it may ingest fewer leaves to meet protein demands (Felton *et al.*, 2009). Animals have a finite amount of time to perform all activities, thus the increase in feeding time we observed had to come at the expense of other behaviours, in this case feeding and traveling. This suggests that the increase in feeding time, coupled with a reduction in travel time, may actually reflect the need for gibbons to move around less while feeding on ubiquitously distributed leaves, compared to fruit which would require greater travel within and between patches. It also suggests they may need to spend more time inactive to cope with the high cellulose content of leaves (Stanford, 1991; Zhou *et al.*, 2007).

Gibbons are known to eat insects (Elder, 2009) and although our study group frequently ate insects (Frechette, pers. obs.), we were unable to determine the influence of insectivory on behaviour as our study protocol did not adequately capture the frequency of insect consumption. We also observed the adult male consuming a baby bird from a nest, and our study group frequently foraged in tree cavities (Frechette, J. pers. obs.). Animal consumption is consequently under represented in our study.

Our study represents the largest dataset for *N. annamensis* and one of the largest generated for *Nomascus* gibbons to date. Overall, our results demonstrate the importance of dietary and behavioural plasticity for these large-bodied and highly frugivorous primates. In

addition, the relationships we observed between behaviour and precipitation are particularly interesting in the context of forthcoming climate change. In improving understanding of the dietary needs of *N. annamensis* and how its activity patterns change seasonally, we anticipate our results will assist efforts to conserve the species. For instance, site-based management efforts for *N. annamensis* should accord high priority to protecting areas with a diverse complement of fruiting trees and particularly important food sources such as figs and dipterocarps.

Acknowledgements

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