Patterns of salt lick use by mammals and birds in northeastern Cambodia

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មូលន័យសង្ខេប

អំបិលធម្មជាតិ ឬខនិជលិត (mineral licks) ជាធនធានមានតម្លៃ ប៉ុន្តែមានដោយកម្រ និងដោយកន្លែងសម្រាប់សត្វព្រៃ។ សត្វមួយចំនួនធំទៅកន្លែងដីប្រោប (salt lick) ដើម្បីស៊ីដី ដែលវាទទួលបាននូវខនិជបន្ថែមជួយសម្រួលបញ្ហាក្រពះ ពោះវៀន និងទប់ស្កាត់ឥទ្ធិពល ជាតិពុលដែលមានក្នុងអាហារ។ ដូច្នេះដីប្រោបត្រូវបានចាត់ទុកជាធនធានដ៏មានប្រយោជន៍ក្នុងរបបអាហារ ជាសារធាតុចិញ្ចឹម និងសម្រាប់សុខភាពសត្វដែលប្រើប្រាស់វា។ តំបន់អភិរក្សវ៉ឺនសៃ សៀមប៉ាងនៃប្រទេសកម្ពុជាតំបន់ដែលមានតម្លៃជីវចម្រុះខ្ពស់ រាប់បញ្ចូលទាំងតំបន់ដីប្រោបមួយចំនួនផងដែរ។ តាមរយៈការដាក់ម៉ាស៊ីនថតរូបស្វ័យប្រវត្តិ (camera trap) នៅប្រាំទីតាំងដីប្រោបនៃតំបន់អភិរក្ស យើងបានស្វែងយល់ពីដំណើរនៃការប្រើប្រាស់ដីប្រោបរបស់សត្វ ក្នុងគោលបំណងវាយតម្លៃពីសារៈសំខាន់នៃធនធានទាំងនេះក្នុងស្ថានប្រព័ន្ធ។ ក្នុងរយៈពេលជាង៥៣០ថ្ងៃនៃការដាក់ម៉ាស៊ីនថតរូបស្វ័យប្រវត្តិ មានថនិកសត្វប្រាំបួនប្រភេទ និងសត្វស្លាបពប្រភេទត្រូវបានប្រទះឃើញនៅទីតាំងដីប្រោប ប៉ុន្តែមានតែថនិកសត្វប្រាំមួយប្រភេទប៉ុណ្ណោះ (ស្វាពីរ សត្វកកេរមួយ និងសត្វចតុប្បាទបី) ដែលត្រូវបានឃើញច្បាស់ថាបានស៊ីដីប្រោប។ អត្រាធ្វើដំណើរ (visitation rate) ប្រេកង់នៃការជួប (encounter frequency) និងរយៈពេលស្ថិតក្នុងទីតាំង គឺខុសគ្នារវាងប្រភេទទាំងនេះ ដូចគ្នាដែរចំពោះលំនាំនៃការផ្តុំជាក្រុម និងពេលវេលាទៅដីប្រោបប្រចាំថ្ងៃ។ ពួកស្វា និងខ្ទីងចំណាយពេលវែងនៅកន្លែងដីប្រោប បង្ហាញថាវាជាអេកូឡូស៊ី សំខាន់សម្រាប់ប្រភេទនេះ។ ខ្ទីង និងឈ្លូសក្រហមត្រូវបានប្រទះឃើញនៅពេលយប់នៅទីដីប្រោប ដែលនេះជាសកម្មភាពខុសប្រក្រតីរបស់ពួកវា។ ទោះបីជាសារៈប្រយោជន៍នៃការស៊ីដីមិនត្រូវបានបញ្ជាក់នៅក្នុងការសិក្សានេះ ប៉ុន្តែប្រេកង់ និងលំនាំនៃការប្រើដីប្រោបដោយក្រុមសត្វរងគ្រោះ (endangered species) និងងាយរងគ្រោះ (vulnerable species) បង្ហាញពីសារៈប្រយោជន៍ចាំបាច់នៃការលិតដី និងឆ្លុះបញ្ចាំងពីតម្រូវការចាំបាច់ឲ្យមានការខិតខំប្រឹងប្រែងការអភិរក្ស និងការការពារតំបន់ទាំងនេះ។

Abstract

Natural salt or mineral licks are valuable, yet spatially limited resources for wild animal populations. Many animals visit salt licks to engage in geophagy, which may serve to supplement mineral intake, ease gastrointestinal issues or buffer the effects of dietary toxins. This makes salt licks beneficial resources for the diet, nutrition and health of the animals that use them. Veun Sai–Siem Pang National Park in Cambodia is an area of high biodiversity value, and includes a number of salt lick sites. By placing camera traps at five salt lick locations within the conservation area, we

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investigated the patterns of lick use by animals to assess the importance of these resources within the ecosystem. Over 530 camera-trap days, nine mammal and three bird species were found to visit the salt licks, but only six mammals (two primates, one rodent and three ungulates) clearly engaged in geophagy. Visitation rate, encounter frequency and duration of visits differed between these species, as did grouping patterns and daily timing of lick visits. Both primates and gaur spent prolonged periods of time at the salt licks, suggesting such sites are an important part of their ecology. Gaur and red muntjacs were found to be nocturnal salt lick visitors, which is atypical of their normal activity patterns. Although the functional benefits of geophagy were not confirmed by this study, the frequency and pattern of use by a variety of Endangered and Vulnerable species demonstrates the significance of the licks and highlights the need to focus conservation efforts on their protection.

Keywords

Camera trap, geophagy, mineral lick, primates, salt-lick.

Introduction

Geophagy, the deliberate ingestion of soil or clay, is a common practice for many animals. Among vertebrates, it has been documented in numerous mammals, including humans (Abrahams & Parsons, 1996), ungulates (Houston *et al.*, 2001; Ayotte *et al.*, 2008; Tobler *et al.*, 2009), primates (Krishnamani & Mahaney, 2000; Ferrari *et al.*, 2008; Rawson & Bach, 2011), bats (Bravo *et al.*, 2008; Voigt *et al.*, 2008), and rodents (Matsubayashi *et al.*, 2007a); as well as in birds (Diamond *et al.*, 1999; Gilardi *et al.*, 1999; Brightsmith & Muñoz-Najar, 2004). Several hypotheses exist to explain the functional benefit of geophagy for animals. One common proposition is that animals use geophagy to supplement minerals that are otherwise lacking in their diets (Ganzhorn, 1987; Moe, 1993; Powell *et al.*, 2009; Dudley *et al.*, 2012). Another suggestion is that geophagy can help alleviate gastrointestinal issues, such as neutralising gastric acidity (Oates, 1978), acting as an antidiarrhoeal agent (Mahaney *et al.*, 1995), or buffering the effects of dietary toxins (Johns & Duquette, 1991; Gilardi *et al.*, 1999). Geophagy might also be used to combat the negative effects of endoparasite infestations (Knezevich, 1998) or increase the pharmacological properties of certain plants (Klein *et al.*, 2008). Currently, no single theory fully explains the occurrence of geophagy; rather, it seems likely that animals consume soil for a number of reasons, which vary with diet, reproductive status, geography, environment and season (Davies & Baillie, 1988; Krishnamani & Mahaney, 2000; Voigt *et al.*, 2008).

Mammals and birds that engage in geophagy often seek out natural mineral or salt licks in their environment. Such licks are spatially-limited resources with soil, clay or ground water rich in minerals (Klaus & Schmid, 1998). They are mostly frequented by herbivorous and omnivorous species, presumably as a consequence of their predominately plant-based diets (Kreulen, 1985). Unlike carnivores that gain sodium from their prey, the intrinsically low sodium in plant tissue means phytophagous species must seek this vital nutrient elsewhere (Dudley *et al.*, 2012). As such, sodium deprivation is often considered a key driver of natural lick visitation (Holdø *et al.*, 2002; Powell *et al.*, 2009; Bravo *et al.*, 2012), but other elements such as calcium and magnesium may also constitute motivating factors (Ayotte *et al.*, 2006; Matsubayashi *et al.*, 2007b), especially in tropical environments where soils (and therefore, plants) are depleted of major cations (Emmons & Stark, 1979; Vitousek & Sanford, 1986).

Maintaining mineral homeostasis is not the only dietary challenge herbivorous species might seek to overcome by visiting natural licks. The consumption of clay has been linked to the adsorption of deleterious chemicals such as tannins, alkaloids or other plant secondary compounds (Gilardi *et al.*, 1999; Dominy *et al.*, 2004), which are especially high in mature leaves and unripe fruit (de Souza *et al.*, 2002; Bennett & Caldecott, 2012). It also adsorbs organic molecules such as fatty acids, which can decrease stomach pH and cause acidosis (Oates, 1978; Kreulen, 1985). Thus, for folivorous and frugivorous species in particular, geophagy at mineral licks may allow animals to exploit potentially harmful plants in greater quantities than they otherwise could, or consume new plant types (Gilardi *et al.*, 1999; Houston *et al.*, 2001; Dominy *et al.*, 2004). The limited nature of salt lick sites can also be advantageous for carnivores, with the increased prey density providing productive hunting grounds (Matsubayashi *et al.*, 2007a).

While mineral licks can provide benefits to animals, their use is not without risk (Klaus & Schmid, 1998). As mentioned, predators (including humans) are known to target lick sites, making visits inherently dangerous (Moe, 1993; Matsuda & Izawa, 2008). The consumption of soil at mineral licks can also expose animals to additional parasites and disease if they eat soil contaminated by faeces or urine (Henshaw & Ayeni, 1971). Animals may also be forced to leave their typical niche to access the resource such as arboreal species spending unusually prolonged periods on the ground (Klaus & Schmid, 1998). Additionally, animals that pursue these resources outside their home ranges can incur energetic costs and lose corresponding feeding and foraging time (Klein & Thing, 1989; Powell *et al*., 2009). The fact that many species seek out these resources despite the risks and costs suggests that they are of high ecological importance (Montenegro, 2004; Blake *et al*., 2011).

Given the potential value of lick sites to animals and the potential anthropogenic risks associated with accessing them, it is imperative that such sites are appropriately protected (Matsubayashi *et al.*, 2007b; Matsubayashi *et al.*, 2011; Molina *et al*., 2014). However, to develop appropriate plans, it is first necessary to understand the diversity of species that use these resources as well as how they are used and their relative importance (Klaus & Schmid, 1998). While such patterns have been widely documented in Africa and the Americas, there are fewer studies from Southeast Asia (Matsubayashi *et al.*, 2007a). In this study, we use camera traps to document species diversity at five salt lick sites within Veun Sai–Siem Pang National Park (VSSPNP, northeastern Cambodia) and describe their patterns of use, with the aim of clarifying the importance of these resources from a dietary and conservation perspective.

Methods

Study Site

Veun Sai–Siem Pang National Park (14°01′ N, 106° 44′ E) consists of approximately 55,000 ha of evergreen and semi-evergreen forest located within Ratanakiri Province, Cambodia (Fig. 1). It borders the larger 320,000ha Virachey National Park and is part of the Indo-Burma Hotspot, a region of global importance for conservation due to its biodiversity values and high threat levels (Myers *et al*., 2000). Initial surveys have reported 60 species of mammals, 130 species of birds and 60 species of reptiles within the reserve (Conservation International, unpublished data). Cambodia has two distinct seasons: the wet season, which occurs from May through October and the dry season from November to April (Thoeun, 2015). It has a mean annual temperature of 28°C (ranging from an average maximum of 38°C in April to an average minimum of 17°C in January) while the mean annual precipitation ranges from 1,200–2,000mm and is governed by monsoons (Thoeun, 2015). To date this site has been managed by the Forestry Administration with support from Conservation International.

Mineral Lick Sites

Five natural mineral licks within the VSSPNP were monitored for this study. These mineral licks represent a small subset of sites involved in a larger camera trap survey that is investigating species diversity in the region. The salt lick sites were selected based on reports from local community members that animals congregate at these locations to eat soil. Five camera traps were placed at these sites and their use as salt licks was confirmed from photographs. Location 1 was a clay bank infiltrated with the roots of trees, while locations 2, 3, 4 and 5 consisted of muddy depressions that were sometimes filled with water. All were surrounded by evergreen forest, except for location 5, which was situated within deciduous forest. All camera traps were located within largely undisturbed forest, but were in relatively close proximity to local ethnic minority villages who know and access these areas (see Fig. 1).

Camera Trap Monitoring

Reconyx PC85 RapidFire™ camera traps were used to document activity at the five mineral lick sites. One camera was placed at the edge of each lick. Cameras were triggered by integrated Passive InfraRed (PIR) motion detectors (with sensitivity on ‘high’) and were set to record three pictures per trigger, with a one second pause between pictures. There was no delay between trigger events. The exact time of each photograph was recorded by the cameras and logged in a database. Species were then identified from the photographs. Cameras were active from January to October 2010 and from January to April 2011. The units were checked approximately once a month for battery condition and damage as well as to download the photos. The total survey effort was 530 camera-trap days.

Data Analysis

Encounter frequencies and relative abundance indices were calculated for each species. Encounter frequencies were calculated by dividing the total number of camera-trap days (total survey effort) by the number of independent records for each species. They are thus expressed as one visit per x number of camera-trap days. Relative abundance indices were calculated by dividing the number of independent records (across all sites) by the total number of camera-trap days (total survey effort) then multiplying by 100, being expressed as the number of independent visits per 100 days. A camera-trap day

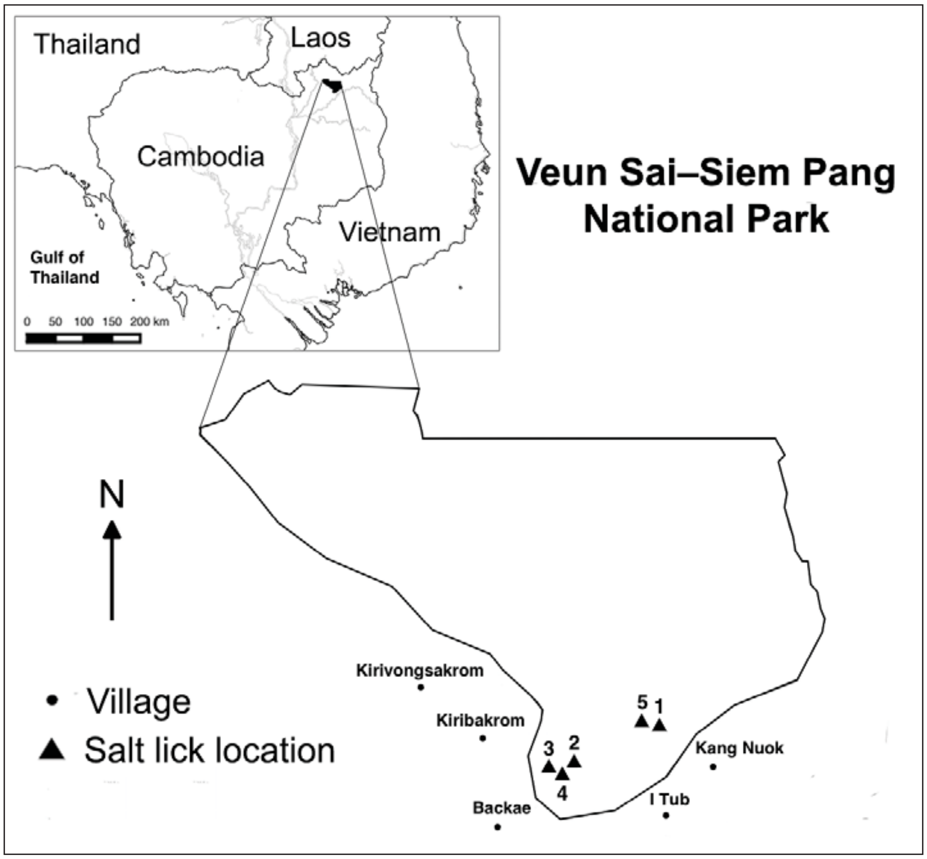

Fig. 1 Salt lick locations within the Veun Sai–Siem Pang National Park, Cambodia.

was defined as a 24-hour period when a camera was active. To avoid issues of non-independence of records, an encounter was considered independent if a period of 30 minutes had elapsed between photographs of the same taxon. While a 30 minute lapse is commonly used in salt lick camera trap studies (e.g., Rawson & Luu, 2011; Edwards *et al.*, 2012; Hon & Shibata, 2013), it was also necessary in this case because animals (especially primates) sometimes disappeared from the camera's frame to access underground portions of the salt licks. Independent encounters from all mineral lick locations were pooled for the analyses.

To describe patterns of use, the following factors were considered for each species: maximum and mean group size, mean visit duration and mean time of day that species visited the licks. The mean visit duration (average time each species spent at licks) was calculated by summing the total time spent at a site during each independent encounter and dividing by the total number of visits. The mean and median times of day (circular means and medians) in which photos were taken was calculated for each species using Oriana version 4 for circular data. They are reported in the results as 24-hour time, with 95% confidence intervals (CI). A Mann-Whitney U test was used to determine if two primate species visited licks at different times of day. Here, the distributions of visit time were similar and the statistics were calculated using SPSS Statistics version 23. A p-value of < 0.05 was considered significant unless otherwise stated.

Rayleigh's Uniformity Test (in Oriana) was used to test the null hypothesis that activity was uniformly distributed throughout the day for each species (cathemerality). Diurnal activity was defined as occurring between one hour after sunrise and one hour before sunset (approximately 07:00–17:00 hrs). Nocturnal activity occurred between one hour after sunset and one hour before sunrise (approximately 17:00–05:00 hrs). Crepuscular activity occurred between one hour before sunrise and one hour after sunrise (approximately 05:00–07:00 hrs), and one hour before sunset and one hour after sunset (approximately 17:00–19:00 hrs). Following Morales (2009), if cathemerality was rejected, species were classified as diurnal if >70% of photos were diurnal and classified as nocturnal if >70% of photos were nocturnal. Species were classified nocturnal-crepuscular if 45–70% of photos were nocturnal and >20% crepuscular, and were classified as diurnal-crepuscular if >45% were diurnal and >20% crepuscular.

Results

Species Assemblage

Over the 530 camera-trap days, 9,462 photos were taken of animals, representing 199 independent wildlife encounters. Nine species of mammals and three species of birds were recorded (Table 1). Together, these represent approximately 16.7% of all species recorded by all camera traps active within the VSSPNP borders (which form a larger camera trapping programme). While nine species of mammals were photographed at the salt lick sites, only six (red-shanked douc, Annamese silvered langur, Malayan porcupine, red muntjac, sambar and gaur) were photographed eating soil (Fig. 2). Unfortunately, geophagy could not be confirmed for any of the birds. Humans (77 encounters) and domestic dogs (9 encounters) were also recorded at the mineral lick sites, but their purpose was not to engage in geophagy. People would use the clear areas as walkways to other destinations, while the dogs were accompanying the humans.

Encounter Frequencies

Encounter frequencies for species that were photographed at the licks but not recorded engaging in geophagy are shown in Table 1; however, these data are not included in the forthcoming analysis. Of the species that engaged in geophagy, encounter frequencies ranged from one visit per 7.5 days (red muntjac) to one visit per

Table 1 Wildlife species recorded at natural salt licks within the Veun Sai–Siem Pang National Park, Cambodia.

Common Name	Scientific Name	No. of Encounters	Relative Abundance[2]	Group Size[3]	Feeding Guild[4]	IUCN Red List[5]
MAMMALS						
PRIMATES						
Red-shanked douc[1]	*Pygathrix nemaeus*	50	9.4	3.1±3.2 (18)	H/F	EN
Annamese silvered langur[1]	*Trachypithecus margarita*	36	6.8	3.6±2.6 (10)	H/F	EN
RODENTIA						
Malayan porcupine[1]	*Hystrix brachyura*	7	1.3	1.4±0.8 (3)	H/F	LC
ARTIODACTYLA						
Red muntjac[1]	*Muntiacus muntjak*	71	13.4	1.1±0.3 (2)	H/F	LC
Sambar[1]	*Rusa unicolor*	9	1.7	solitary	H/F	VU
Gaur[1]	*Bos gaurus*	17	3.2	1.9±1.5 (6)	H/F	VU
Wild boar	*Sus scrofa*	2	0.4	14±16.97 (26)	O	LC
CARNIVORA						
Large Indian civet	*Viverra zibetha*	1	0.2	solitary	C/O	NT
Large spotted civet	*Viverra megaspila*	1	0.2	solitary	O	VU
BIRDS						
Red jungle fowl	*Gallus gallus*	2	0.4	1.5±0.7 (2)	O	LC
Crested serpent eagle	*Spilornis cheela*	2	0.4	solitary	C	LC
Spotted dove	*Spilopelia chinensis*	1	0.2	pair	G	LC

[1] Species recorded engaging in geophagy from photographs.

[2] Expressed as x number of visits per 100 days.

[3] Expressed as mean±SD (max).

[4] H/F=Herbivore-Frugivore; O=Omnivore; C=Carnivore; G=Granivore.

[5] NT=Near threatened; LC=Least Concern; VU=Vulnerable; EN=Endangered.

75.7 days (Malayan porcupine). The two primate species, red-shanked douc and Annamese silvered langur, had the second and third highest encounter frequencies, averaging one visit per 10.6 days and one visit per 14.7 days, respectively. These were followed by gaur with one visit per 31.8 days and sambar with the second lowest frequency of one visit every 58.9 days. Table 1 also provides the relative abundance indices by species.

Species Group Sizes at Licks

A higher percentage (62.6%) of all salt lick photographs were of groups (two or more individuals) as opposed to solitary individuals. The mean maximum group sizes and the maximum group size per species are listed in Table 1. Due to their known gregarious nature, it was not surprising that primates had the largest maximum and mean group sizes. Single individuals accounted for only 38.0% of all independent encounters for the red-shanked douc, and 30.6% for all Annamese silvered langurs. It is unclear, however, if these animals truly were solitary individuals or if the larger group was just out of the camera frame. A known lone male red-shanked douc has been frequently encountered near one of the salt licks.

After primates, gaur had the next largest groups at salt licks. In contrast to primates, however, single individuals accounted for more independent encounters (64.7%) than did groups. The Malayan porcupine and red muntjac photographs consisted mostly of solitary individuals. Groups accounted for only 28.6% and 9.9% of all photographs for these species, respectively. Sambar were never observed in groups.

There were only a few instances where multiple species were photographed visiting the same salt lick site concurrently. These occurred when Annamese silvered langurs joined a group of red-shanked doucs at the same site; a red jungle fowl with red-shanked doucs; and a red jungle fowl with a group of gaur.

Daily Use Patterns

Species differed in how long they spent at the mineral lick per independent encounter. Annmese silvered langurs had the longest mean visit duration (55.0 ± 71.5 min), followed by red-shanked doucs (53.4 ± 49.5 min), then gaur (46.1 ± 102.1 min), red muntjac (7.7 ± 10.3 min), sambar (1.4 ± 2.0 min) and Malayan porcupine (0.8 ± 1.2 min). Visit duration was found to significantly correlate with maximum group size ($r_s = 0.695$, $df = 188$, $p < 0.001$).

Species also differed in the time of day they used the licks (Fig. 3). Photographs of red-shanked doucs and Annamese silvered langurs were usually taken during the morning and afternoon respectively (red-shanked douc: mean = 09:46 hrs, 95% CI = 09:41–09:50 hrs, median = 09:28 hrs); silvered langur: mean = 13:39 hrs, 95% CI = 13:35–13:42 hrs, median = 13:30 hrs), while gaur and Malayan porcupine were photographed on average near midnight (gaur: mean = 00:19 hrs, 95% CI = 00:09–00:29 hrs, median = 23:53 hrs; Malayan porcupine: mean = 00:38 hrs, 95% CI = 00:09–01:06 hrs, median = 01:21 hrs). Both the muntjac and sambar were most frequently recorded at the salt lick in the very early morning (red muntjac: mean = 03:03 hrs, 95% CI = 02:45–03:20 hrs, median = 02:43 hrs; sambar: mean = 01:11 hrs, 95% CI = 00:48–01:33 hrs, median = 01:56 hrs).

A Mann-Whitney U test was undertaken to determine if the two primate species visited the mineral licks at different times of day. Median time of first appearance (per encounter) was significantly different between the species ($U = 227.5$, $p < 0.001$, n[douc] = 50, n[silvered langur] = 36).

Rayleigh's uniformity test demonstrated that species did not visit the site uniformly throughout the day (red-shanked douc: $Z = 2456.236$, $p < 0.001$; silvered langur: $Z = 2808.805$, $p < 0.001$; Malayan porcupine: $Z = 24.209$, $p < 0.001$; gaur: $Z = 685.382$, $p < 0.001$; red muntjac: $Z = 272.252$, $p < 0.001$; sambar: $Z = 76.214$, $p < 0.001$). From these data, the silvered langurs (99.9% diurnal) and red-shanked doucs (94.0% diurnal and 6.0% crepuscular) were classified as diurnal salt lick users. Nocturnal salt lick users included the Malayan porcupine (100% nocturnal) and all of the ungulates: sambar (96.9% nocturnal, 3.1% crepuscular), gaur (85.4% nocturnal, 0.9% diurnal, 13.7% crepuscular) and red muntjac (71.6% nocturnal, 13.4% diurnal, 15.1% crepuscular).

Discussion

To the best of our knowledge, this is only the second published report of species diversity at salt licks within Cambodia, with the first study comprising only a single camera trap and 57 camera-trap days (Edwards *et al.*, 2012). We recorded nine mammal species and three bird species at five salt licks within the VSSPNP. Of these, five of the mammals have been previously recorded at mineral licks in Asia: Malayan porcupine, red muntjac, sambar, gaur and wild boar (Moe, 1993; Matsubayashi *et al.*, 2007a,b; Edwards *et al.*, 2012). No instances of salt lick visitation by red-shanked doucs and Annamese silvered langurs have been reported outside the VSSPNP (Rawson & Bach, 2011). While other species of civets are known to visit mineral licks in Asia (Moe, 1993; Matsubayashi *et al.*, 2007a; Edwards, 2012), this is the first record of *Viverra zibetha* and *Viverra megaspila* visiting such resources. Sim-

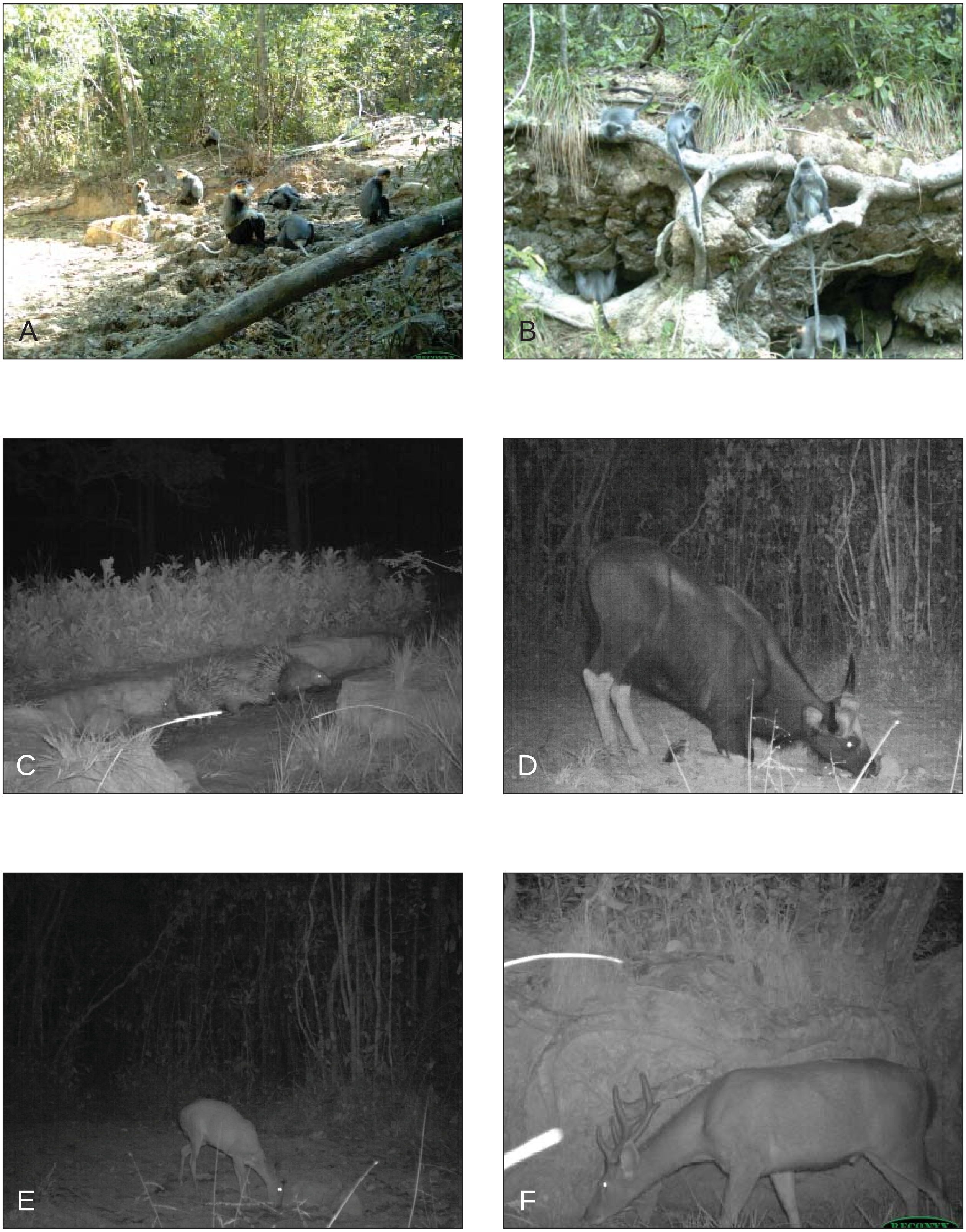

Fig. 2 Photographs of species engaged in geophagy within the Veun Sai–Siem Pang National Park: A) red-shanked douc *Pygathrix nemaeus*; B) Annamese silvered langur *Trachypithecus margarita*; C) Malayan porcupine *Hystrix brachyura*; D) gaur *Bos gaurus*; E) red muntjac *Muntiacus muntjac*; F) sambar *Rusa unicolor*.

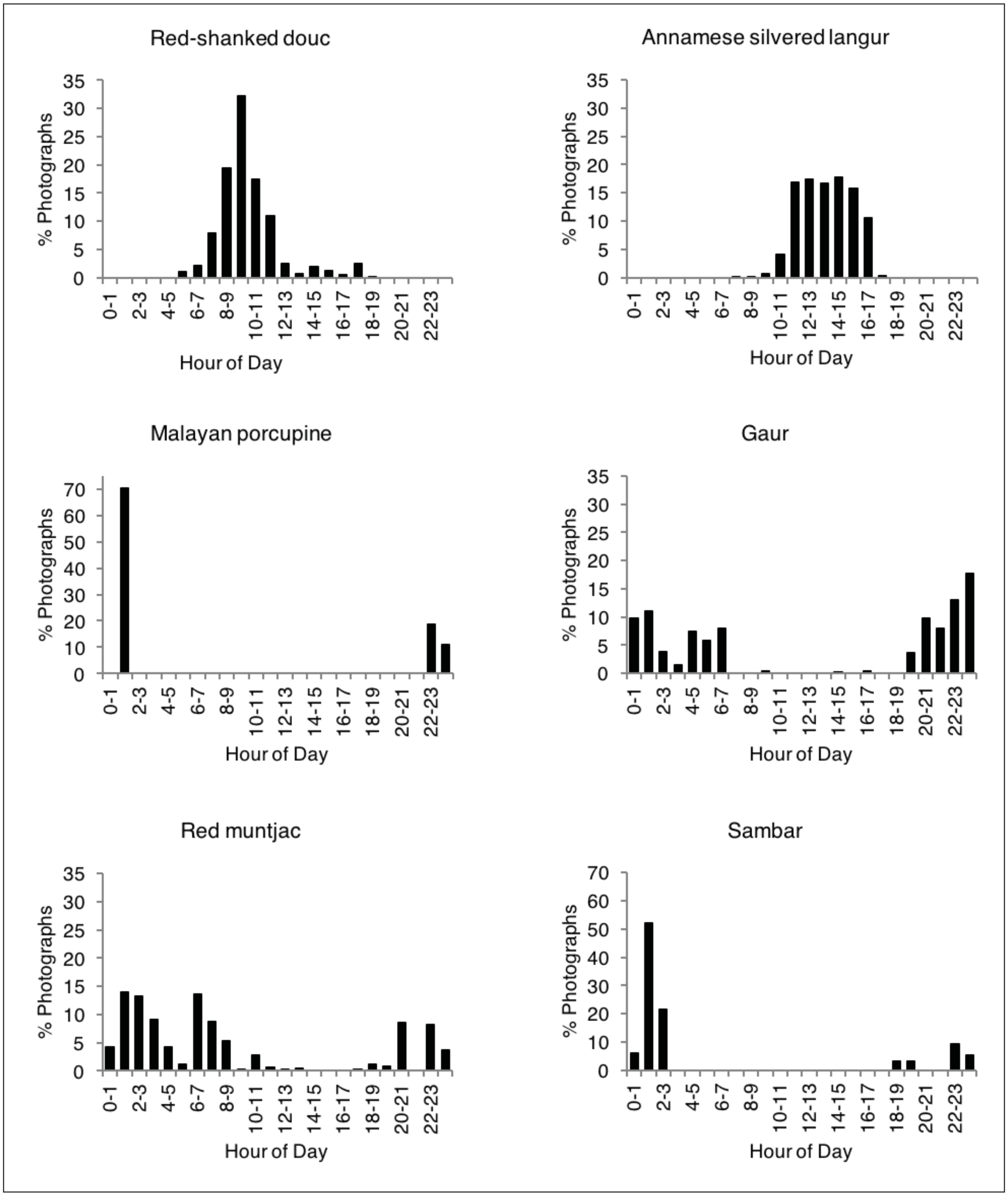

Fig. 3 Histograms representing the daily activity pattern of wildlife species that engaged in geophagy at natural salt licks.

ilarly, bird species within the Phasiniaidae, Accipitridae and Columbidae families have been reported in previous salt lick studies (Diamond *et al.,* 1999; Symes *et al.,* 2005; Blake *et al.,* 2011; Edwards *et al.,* 2012), but *Gallus gallus*, *Spilornis chela* and *Spilopelia chinesis* have not.

Of the species recorded at the salt licks, only six appeared to engage in geophagy. Red-shanked doucs, Annamese silvered langurs, gaur and red muntjacs (all herbivores) visited the sites often and/or for prolonged periods, suggesting the licks may be especially important to the ecology of these species, but soil analyses are required to determine the exact benefit they are obtaining. Civets (carnivores) were photographed twice at the licks, but on both occasions they appeared interested only in drinking water that had pooled at the site. All the birds recorded at the sites had very short visits (with the exception of the crested serpent eagle, which spent a long time preening).

Mammals tended to visit the salt licks according to species-typical grouping behaviour (either as solitary individuals or groups), which suggests the licks did not serve a gathering function or act as a mating venue (Morales, 2009). However, across species, group size was found to correlate with visit duration, suggesting those species with larger groups may be better able to dominate this spatially limited resource or better protect themselves against predation, making it less risky to stay at the site for longer periods.

Other studies have reported increases in group size at salt licks for primates. In a study of white-bellied spider monkeys *Ateles belzebuth* in Western Amazonia, Link & Di Fiore (2013) found that these primates formed larger groups than normal when visiting salt lick sites because the licks were perceived as areas of high predation risk and larger groups provided some defence against this (Link *et al.,* 2011). While we did not find a similar pattern, there was one incident of a polyspecific association between the two primate species, which could be the result of perceived predation risk; however, we caution against drawing a strong conclusion based solely on one case. Generally, the primates visited the site at different times of day: red-shanked doucs frequented the site in the morning, and Annamese silvered langurs in the afternoon. This could represent an aspect of niche separation, designed to avoid direct competition for the resource (Rawson & Bach, 2011).

Gaur also visited the salt licks in groups of up to six individuals. Although the basic gaur social unit is a female-juvenile pair (Duckworth *et al.,* 2008), temporary assemblages or maternal herds have been reported in some regions (Steinmetz *et al.,* 2010; Ramesh *et al.,* 2012). Nonetheless, given the presence of known gaur predators at VSSPNP (such as leopards, dhole and historically, tigers), the larger groups could also represent a strategy to lower hunting risk. Evidence that the gaur are under pressure in this area additionally comes from their daily use patterns, which were more nocturnal than typical. In a study of mammals and birds, Blake *et al.* (2013) found that diurnal activity was reduced at salt lick sites with higher levels of hunting compared to hunting-free controls, with this particularly true for red brocket deer *Mazama americana*. Similarly, gaur in India become predominately nocturnal in response to severe habitat disturbance and human encroachment on their habitat (Duckworth *et al.,* 2008), as have banteng *Bos javanicus* in Cambodia (Chan & Gray, 2010). These pressures also may have affected the red muntjac within VSSPNP, as their activity patterns too are usually more diurnal/cathemeral than our data suggests (Kawanishi & Sunquist, 2004; Hon & Shibata, 2013).

Although the cause of salt lick visitation was not investigated in this study, the relatively high visitation frequency of six mammal species does suggest they are ecologically important resources. With six out of the 12 recorded animals listed as Near Threatened, Vulnerable, or Endangered by the IUCN (2015), it is important such resources are adequately protected to safeguard lick users against human hunting, habitat disturbance and snares. In VSSPNP, hunting hides have been detected at salt lick sites, presumably to take advantage of animals congregating in these areas, and as such enforcement efforts should aim to suppress such behaviour. To further understand the importance of salt licks on species ecology within Cambodia, additional research should be conducted, with studies that include soil analyses being a specific priority.

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