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Distribution and Habitat of Assamese Macaque *Macaca assamensis* in Lao PDR, Including its Use of Low-altitude Karsts

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Abstract: The distribution and ecology of Assamese macaque *Macaca assamensis* remains little studied in South-east Asia. This review collates historical and recent records to clarify its range and habitat use in Lao PDR. Contrary to many standard sources limiting Assamese macaque's range to the north and center of the country, it occurs well into the southern part. In the country's three physiographic units, it is widespread in the northern highlands and the Annamite range, but seems absent from the Mekong plain. Most records are from hill evergreen forest above 500 m, consistent with standard literature, but the species occurs down to plains level (200 m) on karsts (at least in areas south of 16°58'N). The few records from below 500 m off karst are all in rugged terrain, but even so non-karst rugged land below 500 m seems to be only rarely used. Ecological overlap with northern pig-tailed macaque *M. leonina* and with Rhesus macaque *M. mulatta* is very limited in Lao PDR. In the long-term, hunting and forest encroachment may threaten Assamese macaque in Lao PDR, but it is much less imminently at risk in the country than are most gibbon and colobine species.

Key Words: Assamese macaque, Macaca assamensis, field identification, geographical distribution, habitat use, Laos, limestone

Introduction

Assamese macaque Macaca assamensis occurs from central Nepal east through the Himalaya to southernmost China and north and central South-east Asia (Fooden 1982). It has never had intensive field study anywhere in South-east Asia, or, barely, in South Asia (Mitra 2002, 2003), so remains little known for such a widespread monkey (Fooden 1982; Eudey 1991; Rowe 1996). It has conventionally been seen as a highland species: Lekagul and McNeely (1977), for example, called it "an upland macaque, generally found in forested areas above 500 m to as high as 3,500 m". Fooden's (1982) comprehensive review found most records from 150–1,900 m, with some up to 2,750 m (extended to 3,100 m by Fooden 1986), and a single, disjunct, record from sea-level (see below). A recent survey in Bhutan found Assamese macagues down to 600 m (Kawamoto et al. 2006); Choudhury (2008) referred to occurrences as low as 100 m but neither detailed nor discussed the record(s). Specifically in South-east Asia, records traced by Fooden (1982, 1986) were almost solely in mid- and high-elevation forest, with the lower hill records coming from South Asia.

Consistent with Fooden's (1982) conclusions, Ruggeri and Timmins (1997: 1) wrote that in the southern two-thirds of Lao PDR, "[Assamese macaque is] found predominantly in the evergreen forests of the Annamites [mountains]" but continued "it appears to be the most common species of macaque within areas of karst." Yet the relevant primary survey reports contain little information on this karst use in Lao PDR, this habitat use is omitted from some recent compilations (for example, Francis 2008), and the species was not even mentioned in a review of South-east Asian karst biota by Clements *et al.* (2006).

The present document therefore presents the records of Assamese macaques in Lao karst, in the context of as full a compilation as practicable of the species's records from all habitats in the country.

Survey areas and methods

Lao PDR is a landlocked country of 236,800 km², of three biogeographic divisions: the mountainous northern highlands and Annamite range, and the mostly lowland Mekong plain. Historical mammal collections in the country were few and,

mostly, small (for example, Osgood 1932; Delacour 1940). During 1992–1998, many mammal surveys based on direct observation, mostly in support of the national protected area (NPA) system declared in 1993 (Berkmüller *et al.* 1995), clarified the status of numerous species across the country (Duckworth *et al.* 1999). The first four years of these surveys (late 1992 to mid-1996) generated over 300 sightings of diurnal primates (Ruggeri and Timmins 1997), although such survey activity has declined greatly since 1999. This review collates records of Assamese macaque from Lao PDR until early 2010. The many camera-trap photographs from Nakai–Nam Theun NPA in the 2000s, however, have not been reviewed, given the existence of many field records from this area in the 1990s.

Reviews of the Lao conservation status of red-shanked douc Pygathrix pygmaeus, diurnal squirrels (Sciuridae), François'-group leaf monkey Trachypithecus francoisi (sensu lato) and Lao leaf monkey T. (f.) laotum detailed the locations, methods and intensities of wildlife surveys in the 1990s-2000s (Timmins and Duckworth 1999, 2008; Duckworth et al. 2010a; Steinmetz et al. 2011). Of relevance to monkeys, most surveys were based upon direct daytime observation, unconstrained by any rigid search protocol, supplemented by searches for pets and remains of hunted animals in the field and in villages, and judicious use of local views on mammal status. For some surveys the text below expresses effort in terms of 'person-weeks'; the sum of all the field time of independently operating observers on the survey in question. A single observer for four weeks, a team of two making field observations together for four weeks, a team of two operating independently for two weeks, or a single person surveying half time for eight weeks (with, say, the other half spent in village-based activities) would all count as four person-weeks.

Five species of macaque inhabit Lao PDR (Duckworth et al. 1999) and their identification in the field requires care. During the 1990s, many encounters were left unidentified to species: the monkeys' habitual shyness meant that, if the animals were seen at all, it was often only poorly. Assamese macaque has a long history of range confusion through misidentification, discussed in detail by Fooden (1982). More recently and concerning Lao PDR, the photograph placed on the internet in support of the identification of Assamese macaque in the camera-trap survey of Nam Kading NPA reported by Ahumada et al. (2011) was of a northern pigtailed macaque M. leonina, a species not identified by them at all. However, this misidentification was merely one of several elementary identification errors revealed by their placing their images on the internet; in reality, reliable identification of this species on camera-trap photographs is perfectly possible provided basic cares are taken.

In Lao PDR, the main confusion risk for Assamese macaque is Rhesus macaque: the two species have similar length tails, differing from those of the other three Lao macaques. Rhesus has rich rufous hindquarters contrasting with its non-rufescent forequarters, whereas Assamese has more uniform brown upperparts (often lacking any rufescence, but sometimes quite golden or even rufous) somewhat

darkening to the forequarters, without contrasting russet on the haunches. It also has a call apparently not given by other Lao macaques: a high-pitched eyou, rapid and somewhat gull Larus-like (alternatively transcribed, in Myanmar, as eeoow!, recalling a deflating lorry air-brake). Diagnostic, but often not visible in the field, is the fore-crown hair arrangement, with a short 'parting' resulting from diverging hair tracts (versus a uniformly upwardly directed hair tract across the fore-crown of Rhesus). Assamese also seems always to lack two features sometimes shown by Rhesus, a darker cap and a red (often lurid red) perineal region; and, when present, its lengthy pale beard is diagnostic. Also, pale ischial callosities of Assamese macaques can be prominent at surprisingly long range. Tails can differ between the species, with that of the Rhesus macaque sometimes somewhat bicolored. The southern half of Lao PDR holds apparent intergrades between Rhesus and long-tailed macagues M. mulatta and M. fascicularis, which may have medium-length tails but reduced or absent rusty tones on the hindquarters (Fooden 1996, 1997). They are generally somewhat paler than more northern Rhesus macaques (Evans et al. 2000) and, as found by Eudey (1980) in part of Thailand, invite confusion with Assamese macaque.

Most identifications used several characters, and animals were generally observed as critically as their shyness allowed; some identifications had to remain provisional. Identifications from the early 1990s surveys were reviewed by RJT in the late 1990s and again during preparation of this manuscript, with increasing understanding of intraspecific variation in Assamese and Rhesus macaques in Lao PDR through extensive field experience (including in adjacent Vietnam), observations of many captive macaques of all Lao species, and review of literature. Two provisional Assamese macaque identifications were reassigned to Rhesus macaque, one corrected in Evans *et al.* (2000), the other being a 1996 observation from north of the Nam Theun below the Nam Theun 2 dam site (Dersu 2008). Several Assamese macaque records considered provisional at the time of survey were confirmed.

Village-derived information about macaques is not used here because the present authors, after experimentation, had no confidence that it could be used consistently for reliable species identification (see, for example, Duckworth et al. 2010a). Moreover, after far more extensive discussion with local people in several parts of Lao PDR, a surveyor much practiced in such techniques and fluent in Lao, Steinmetz (1998a: 7), wrote that "classification [to biological species] of the other local terms for macaques [additional to unmodified ling, which was linked for the survey area in question to pig-tailed macaque] is more obscure ... For these reasons I will not attempt to sort out this confusion at this point... Field observation is required before definitive matches can be made". Similarly, after a nine-month village live-in, discussion-focused study in two Hmong villages of northern Thailand (adjacent to Lao PDR), Tungittiplakorn and Dearden (2002: 60) concluded that "an attempt to differentiate between species of monkeys was abandoned after many different and conflicting names and descriptions were received. One group

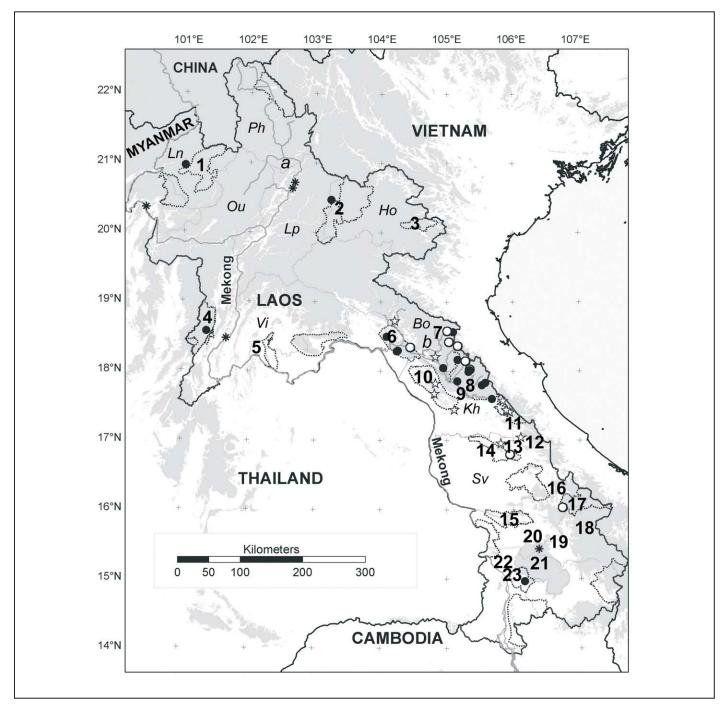


Figure 1. Lao PDR, showing localities mentioned in the text and records. Background shading shows land over 500 m. All national protected areas (NPAs) within the area covered, but only those provincial protected areas (PFAs), provinces, districts and rivers referred to in the text, are shown. The concentration of Assamese macaque records in central Lao PDR relative to the paucity further north at least mostly reflects distribution of survey effort, rather than relative abundance of Assamese macaques.

- modern record of Assamese macaque, away from karst, identification confirmed;
- o modern record of Assamese macaque, away from karst, identification provisional;
- ☆ modern record of Assamese macaque, on karst, identification confirmed;
- * historical record of Assamese macaque.

Provinces: Bo = Bolikhamxai; Ho = Houaphan; Kh = Khammouan; Ln = Louangnamtha; Lp = Louangphabang; Ou = Oudomxai; Ph = Phongsali; Sv = Savannakhet; Vi = Vientiane.

Rivers: a = Nam Ou; b = Nam Kading (known as Nam Theun in it upper reaches).

Numbered areas: 1, Nam Ha NPA; 2, Nam Et–Phou Louey NPA; 3, Nam Xam NPA; 4, Nam Pouy NPA; 5, Muang Sangthong; 6, Nam Kading NPA; 7, Nam Theun Extension pNPA; 8, Nakai–Nam Theun NPA; 9, Nakai plateau; 10, Phou Hinpoun NPA; 11, Hin Namno NPA; 12, Laving-Laveun PPA; 13, central Muang Vilabouli; 14, Phou Xang He NPA; 15, Xe Bang-Nouan NPA; 16, Ban Somoy; 17, Xe Sap NPA; 18, Dakchung plateau; 19, Phou Theung plateau; 20, Ban Thateng; 21, Bolaven plateau; 22, Pakxe; 23, Dong Hua Sao NPA.

that was particularly difficult to identify was the macaques (genus *Macaca*)." These difficulties no doubt reflect the wide intraspecific age- and sex-related variation in appearance in macaques; and local perceptions of Assamese macaque as a unit distinct from other macaques is likely to be hindered by its lack of remarkable diagnostic visual characters. Thus, although interview-based surveys including macaques were conducted in parts of Lao PDR during the 2000s, their results are not considered here; none that we have seen documented any meaningful quality control assessment of reliability of macaque identifications to species, nor any triangulation of their results against field records.

Results and Discussion

General distribution in Lao PDR

Historical Assamese macaque records from Lao PDR were reviewed comprehensively by Fooden (1982). We have traced none other than the five specimens he listed (Appendix 1). Four were from the northern highlands, and the fifth from the Bolaven plateau in the south of the country. This southern specimen came from J. Delacour, who sometimes purchased animals in markets, but it seems unlikely to have been transported onto the plateau from anywhere else.

The 1990s-2000s surveys generated records from typical hill evergreen forest across much of the country (Appendix 2). These rather few records risk implying a misleading scarcity of the species in Lao PDR: that the field identification characters are subtle and need careful checking, yet animals are generally vigilant and shy, means that a lower proportion of actual Assamese macaque encounters will have been identified than with the other macaque species. And in the northern highlands it was simply very difficult to see and identify any macaques at all in the 1990s: in Nam Et-Phou Louey NPA macaques, always unidentifiable, were seen only four times during 14 person-weeks of field survey in 1998, and the only macaque firmly identifiable to species was a recently shot bear macaque M. arctoides (see Davidson 1998); the Assamese macaque group seen in Nam Ha NPA was the only macaque sighting firmly identifiable to species in 10 person-weeks, with only two sightings of unidentified macaques (Tizard et al. 1997); and there seem to have been no macaque sightings at all in six person-weeks at Nam Xam NPA in 1998 (Showler et al. 1998). A roadside survey of pet macaques in several northern highland provinces in May 2006 located 11, of which six were Assamese macaques (Hamada et al. 2007). Although the origin of these cannot be known, the high species proportion is consistent with the 1990s suggestions that this is the most numerous macaque of Lao hills and mountains. Hamada et al. (2007) found no more than two individuals of any other macaque species.

The Annamite range of Bolikhamxai and Khammouan provinces provided many records in the typical hill evergreen forest habitat. The Navang logging road (illicit; closed shortly after construction, and never used for timber extraction) into the heart of Nakai–Nam Theun NPA perhaps best indicated

'natural' status given the excellent long-distance viewing opportunities and (then) limited hunting of primates in the area: in 1996 the species was seen several times per week, spread across the upper 5 km of road surveyed (Duckworth 1998).

The Bolaven plateau in South Lao PDR, biologically a western outlier of the Annamites, holds Assamese macaque, but occurrence is not yet confirmed in the main Annamite range at these latitudes, with only one, provisional, field record. Additionally, two skulls from around the Dakchung plateau (c.15°30'N) of animals shot in 1993 are probably Assamese macaques (Bergmans 1995), and a captive that Steinmetz *et al.* (1999) saw in Ban Somoy (16°17'N, 106°54'E) is very likely to have been sourced locally (R. Steinmetz *in litt.* 2010). Kawamoto *et al.* (2006) recorded a pet Assamese macaque of unknown origin from Pakxe (15°07'N, 105°48'E), in the lowlands just west of the Bolaven plateau; but Pakxe is enough of a trading node that this should not be assumed to have been taken locally.

Despite extensive survey (see effort figures in Timmins and Duckworth 1999, 2008) in the several NPAs of the Lao Mekong plains, there are no records of this macaque from them, nor from the hills arising in their west, which are all rather low. And there is only one, evidently exceptional, from the well-surveyed Nakai plateau (Evans *et al.* 2000; Dersu 2008; U. Streicher *in litt.* 2010), a gentle plateau of 1,250 km² amid the Annamites (Dersu 2008) with Assamese macaque records in the hilly parts of the catchment both upstream and downstream of it.

The paucity of solid records (of any macaque species) from the northern highlands fits a general tendency for hunting-sensitive diurnal quarry species to be found much less often during direct survey there compared with areas in and south of the Nam Kading catchment (Fuchs *et al.* 2007; Duckworth 2008; Timmins and Duckworth 2008). This reflects differing

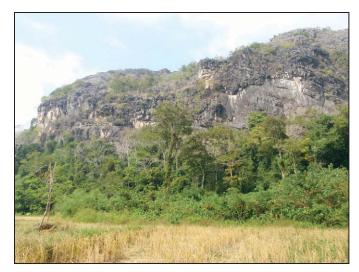


Figure 2. Pha Lom, north-east Savannakhet province, Lao PDR, 14 November 2008. Photograph by I. A. Woxvold. A small (*c*.800 m long × 250 m wide), isolated karst amid agriculture and degraded plains forest. In this landscape, Assamese macaques have been recorded only on the karsts.

patterns of hunting and, perhaps, use of forest for agriculture, which stem from the differing ethnic make-up across the country. The pattern is unlikely to reflect any inherent property of forests or climate, although historical collection effort was too meager to demonstrate that Assamese macaques were formerly more common in the northern highlands.

Karst records

Table 1 details records of Assamese macaque on Lao karst. The first record came during a short visit to Phou Hinpoun (= Khammouan Limestone) NPA, an area predominantly of massive karst, in 1994. Two subsequent short surveys of this NPA regularly found Assamese macaques on karst, and around this time there were also records from two nearby karsts, Pha Khok and Sayphou Loyang.

Hin Namno NPA is the only other NPA predominantly of karst. Here, single groups were found at all karst sites visited during a short survey in 1996, except for the only brief forays in the southern part of the NPA (Timmins and Khounboline 1996). A lengthier survey (7 person-weeks) during February–March 1998 (Walston and Vinton 1999) yielded six field sightings given as confirmed and three as provisional,

a single freshly shot individual, and a village captive; some sightings were specifically noted as in limestone forest but it is not clear how many were. No information is given about altitude or precise localities. Moreover, J. L. Walston (*in litt*. 2010) cautioned that, reflecting the political complexities of this survey, some of the large mammal information incorporated may have been unreliable. This plausibly involved misidentification of Assamese macaques as other macaques, rather than vice versa, reflecting some team members' (whose survey time is excluded) belief that Assamese macaque is extremely rare.

Karsts were little surveyed from 1999 to 2007, but a 2008 visit to the southernmost canopy-breaking outcrops in Lao PDR, in western and central Muang (= district of) Vilabouli (north-east Savannakhet province), again found Assamese macaques on karst. Almost every protracted watch of a karst massif from neighboring plains (often rice fields) yielded a sighting, and the animals were indifferent to noise and movement of the people below. The animals were a good deal shyer when found by an observer himself within forest on Pha Kat's lower slopes. These Savannakhet records are of particular interest in several ways: some animals were almost

Table 1. Records of Assamese macaque Macaca assamensis from karst in Lao PDR.

Site name, location	Co-ordinates and altitude(s) of sighting	Date(s) of sighting	Reference(s)	Other notes
Phou Hinpoun NPA				
Near Ban Lak-91	17°27'N, 105°07'E; c.300 m	23 May 1994	Evans et al. 2000	A group crossed a wooded karst cliff
Khuadin	17°50'N, 104°50'E; 220–300 m	7 & 8 Feb. 1996	Timmins 1997; RJT	Single groups in karst both days
Khuadin	17°50'N, 104°50'E; 250–270 m	17–19 Mar. 1998	Steinmetz 1998b, R. Steinmetz <i>in litt</i> . 2010	A group amongst huge boulders in karst forest
Kouan Houy	17°41'N, 104°49'E; <i>c</i> .200 m	1–5 Apr. 1998	Steinmetz 1998b, R. Steinmetz <i>in litt</i> . 2010	A group on sparsely vegetated sheer karst, rising above the semi-evergreen forest
Hin Namno NPA ²				
Near the Houay Clocc	17°26'N, 105°55'E–17°25'N, 105°57'E; <i>c</i> .400–550 m	1, 3 & 4 Jan. 1996	Timmins & Khounboline 1996; RJT	
Near the Houay Pakha	17°27′N, 105°54′E; 250 m	5 Jan. 1996	Timmins & Khounboline 1996; RJT	
Houay Talee	17°35′N, 105°51′E; <i>c</i> .350–600 m	8 Jan. 1996	Timmins & Khounboline 1996; RJT	
Near the Houay Phasong	17°36'N, 105°50'E; 260 m	13 Feb. 1998	P. Davidson in litt. 2011	Two in rather deciduous forest near, but not on, karst
Near the Nam Ngo	17°30'N, 105°51'E; 200 m	15 & 16 Feb. 1998	P. Davidson in litt. 2011	A group in semi-evergreen forest at base of karst
Muang Vilabouli				
Pha Lom	16°58'N, 105°49'E; <i>c</i> .400 m	13 Nov. 2008; 15h15–15h30	JWD	A party of 13 (with one part-grown animal) moving across the higher, open, karst
Pha Lom	16°58'N, 105°49'E; <i>c</i> .400 m	3 Dec. 2008; 17h15	JWD	A troop of at least seven behaving as on 13 November
Pha Kat	17°03'N, 106°07'E; <i>c</i> .450 m	16 Nov. 2008; afternoon	JWD	Three sightings of single vigilant animals (?one individual) on the high west face
Pha Kat	17°03'N, 106°07'E; 260 m	20 Nov. 2008; 10h00	JWD	At least ten at a fruit tree in the evergreen forest growing from the karst base
Pha Kat	17°03'N, 106°07'E; 260 m	21 Nov. 2008; c.11h00	JWD	At least eight in a fruit tree in basal evergreen forest, then on karst face, c.1 km north of previous day's observation
Other areas				
Pha Khok, north of Nam Kading NPA	18°44'N, 104°13'E; 525 and 650 m	20 Mar. 1995	Evans et al. 2000; RJT	Perhaps two sightings of one group
Sayphou Loyang, near Ban Poung	18°14'N, 104°50'E; 725 m	13 May 1995	Evans et al. 2000; RJT	A group seen

¹ = Ban Lak Kao; date incorrectly given as 1995 in Evans et al. (2000).

² Does not detail most of the reported observations from a lengthier survey of Hin Namno NPA in 1998; see text.

at plains level; Pha Lom lacks any tall evergreen forest, supporting, where not bare rock, stunted open pachycaulous deciduous woodland (Fig. 2; shown in close-up in Woxvold et al. 2009: Plate 4); and these karsts, unlike those in Phou Hinpoun and Hin Namno NPAs, are small outcrops isolated amid non-karst habitat: even Pha Kat, the biggest, is only $c.2.5 \, \mathrm{km}^2$. No other macaque was observed on these karsts, although pig-tailed, Rhesus and bear macaques were all found in the survey area (Duckworth et al. in prep.).

These records of karst-living Assamese macaques come from three contiguous provinces in central Lao PDR (Savannakhet, Khammouan and Bolikhamxai). Karsts are also extensive in the country's northern highlands, but—here lying largely outside the national protected area system—have been barely surveyed for mammals, and their macaque species are unknown.

In sum, karst use is typical of Assamese macaque in Lao PDR, and this macaque is a feature of Lao karst landscapes, at least in the central provinces.

Overall habitat use

Ruggeri and Timmins (1997: 1) stated that Assamese macaque was "rarely encountered in heavily degraded or semi-deciduous habitats" in Lao PDR, and subsequent records away from karst gave nothing to modify this conclusion. Nearly all Lao records traced were from evergreen forest, consistent with Fooden's (1982) profiling of it as a species that is almost completely arboreal and strongly associated with dense evergreen forest. He found that records from deciduous areas, bamboo and cultivation were all from close to this main habitat. Lao records outside evergreen forest comprised several from karst supporting largely deciduous vegetation (both Pha Lom and Pha Kat, Savannakhet province), and from the foot of the Bolaven plateau slopes in Dong Hua Sao NPA where the animals were in semi-evergreen forest with a high proportion of deciduous trees.

Away from karst, most records came from above 500 m, with the lowest from somewhere between 200 and 400 m (imprecisely recorded; and only provisionally identified), and the next lowest from 400 m. By contrast, karst records came down to 200 m, with occurrence at six sites in the 200-400 m band. The use of karst at altitudes lower than typical in nonkarst habitats may reflect its steep topography. Assamese macaques seem effectively absent from non-rugged terrain below about 500 m, as shown by the several surveys in the Lao range of Assamese macaque (i.e., Bolaven plateau and northwards) which did not find it despite a fair number of records of other monkeys and of gibbons: Nakai plateau (Dersu 2008 and references therein; one subsequent record of Assamese macaque); Xe Bang-Nouan NPA (Evans et al. 2000); Muang Sangthong, Vientiane municipality (Duckworth 1996); Phou Xang He NPA outside Phou Hinho (Duckworth et al. 1994); non-karst parts of western and central Muang Vilabouli, Savannakhet province (Duckworth et al. in prep.); and the Phou Theung plateau (Timmins 2009). There are also substantial areas below 500 m in Lao PDR on rugged

terrain that are not karst. These have not been as well surveyed as karsts at comparable altitude, but in sum the paucity of records from such altitudes in Nam Kading NPA (Evans *et al.* 2000, Timmins and Robichaud 2005), two production forest areas in Vientiane province (Suford in press), Laving-Laveun Provincial Protected Area (Duckworth *et al.* 2010b), and the Phou Hinho part of Phou Xang He NPA (Duckworth *et al.* 1994), suggests a general scarcity in such habitat. The cited surveys of all these sites detected other species of monkey and gibbons fairly often.

Karts's expanses of bare rock (bigger and more numerous than in most non-karst habitats) may themselves be important to Assamese macaque. In Nepal, sleeping sites in hill evergreen forest are typically rocky cliffs, usually devoid of trees and shrubs, and presumably selected to minimize risk of attack by predators (Chalise 2003); in West Bengal the species was said to prefer rocky terrain and hill slopes (Mitra 2002); and seven of eight sightings in Mizoram, India, by Raman *et al.* (1995: 60) were "along cliffs with primary vegetation," the other being "close to the cliff face." Although in Bhutan "rocky cliffs with sparse vegetation" are an apparently minor habitat (Choudhury 2008: 66), field contacts with the species in western Thailand were in forest by or on rocky mountains (Eudey 1991).

At lower altitudes, Assamese macaques may require steep cliffs; but they do not at higher altitudes: in parts of interior Nakai-Nam Theun NPA, the species occurs far from cliffs. Cliffs might serve as sleeping sites. Although Fooden (1986) traced no information on such sites and speculated that the species would be found to sleep in trees, Eudey (1991) thought that in Huay Kha Khaeng Wildlife Sanctuary it slept in protruding crags or the large trees adjacent to them, and the subsequent information (above) from other countries indicates use of cliffs as sleeping sites. There remains no information on where Assamese macaques sleep in Lao PDR; Walston and Vinton (1999: 23) wrote of "two groups seen at sleeping sites at Khoaymep forest," but no details are now available, including confirmation of identification (J. L. Walston in litt. 2010). In Lao PDR, the karst itself is used for travel (even over hundreds of meters) and to provide look-out perches when most of a troop is feeding in karst forest, from which most records in karst landscapes came.

Karst and low-altitude records from other countries

There are various records from karst landscapes in Vietnam (Nisbett and Ciochon 1993), notably Phong Nha–Ke Bang National Park (Timmins *et al.* 1999; Haus *et al.* 2009), and also the Nui Giang Man area, Di Gia Nature Reserve and Na Hang Nature Reserve (Nadler *et al.* 2004). These documents do not detail altitudes of observation and are rarely explicit whether macaques were on the karst: therefore it is not possible to tell whether there is the same habitual karst use, and a similar difference in altitudinal occupation between karst and non-karst areas, in Vietnam as in Lao PDR. In Myanmar, Anderson (1879) noted a large group of Assamese macaques on the bank of the Irrawaddy downstream

of Bhamo (24°16′N, 97°14′E), below a huge limestone cliff. The Irrawaddy here is at *c*.100 m, indicating lowland karst use also in that country. These animals were artificially provisioned, so it is unclear whether this was their natural habitat. In Thailand, detailed information comes from three karsts around Buddhist temples, where Assamese macaques occur down to 400 m (Aggimarangsee 1992); as in Lao karst, this is perhaps rather low for the species in South-east Asia. Off karst in Thailand, Assamese macaque was encountered regularly in dry evergreen forest in Phu Khieo Wildlife Sanctuary during a study at 600–800 m (Borries *et al.* 2002), and in an altitudinally wide-ranging study in Huai Kha Khaeng Wildlife Sanctuary it was found between 700 and 1,400 m (Eudey 1991); but little else specific seems to be available on altitudinal distribution in the country.

A superficial check of information from elsewhere in the species' range showed no discussion of karst use, although occasional reference is made to occurrence in areas containing some karst (for example, Yimkao and Srikosamatara 2006). Several other records indicate lowland occupancy, for example, on the floodplain of Dibru-Saikhowa National Park, Assam, India (Choudhury 2001). There is one essentially sea-level record: from the Sundarbans coastal swamps of Bangladesh, c.50 miles east of Calcutta (Anderson 1872). Fooden's (1982) careful review found no reason to doubt this record. In fact, Anderson's (1872) account has several strong points: having heard rumors of two sorts of macaques from local inhabitants of the Sundarbans, the descriptions of which fitted Rhesus and Assamese macaques, he sent his collector to the area, who returned with undoubted examples (identifications re-validated a century later by Fooden's own examination) of both species. This contemporary awareness means a curatorial error in the interim (for example, erroneously inferred locality, or mis-association of specimen and tag) can be discounted. Nonetheless this record is extraordinary, causing doubts in some present-day quarters. Nearby there are neither modern records of Assamese macaque (despite fairly heavy wildlife survey and research presence), nor any hills, even small ones, let alone karst. The nearest hill-forest where Assamese macaque would be expected (and indeed occurs) lies approximately five times the distance further east of Calcutta, so a mistake over locality seems unlikely (Md. Anwarul Islam in litt. 2010, P. M. Thompson in litt. 2010). The only possibility for error seems to be a dishonest collector who for some reason falsified the locality.

Ecological overlap with Rhesus macaque

Fooden (1982) concluded that Assamese macaque was ecologically parapatric with, respectively, pig-tailed and Rhesus macaques. Recent Assamese macaque records in Lao PDR overlapped geographically and altitudinally with both these species, but ecological separation may well nonetheless be strong. This review traced no Lao records of Rhesus macaque in karst; it occurs predominantly in stream-side and degraded areas. In these latter habitats Assamese macaque has not been recorded in Lao PDR, but there is some overlap in

adjacent countries. In the Hukaung valley of northern Myanmar, along the Tarung Hka (a river), on 21 January 2006 a troop of about 20 Assamese macaques was seen on low bedrock exposed from the river's banks, with several down at the water's edge, at c.26°47'N, 96°31'E; and that evening a group of a score or so was seen apparently settled for the night in a streamside giant tree, at c.26°45'N, 96°29'E. Yet Rhesus macaques were commonly observed along this river, and others, in the Hukaung valley (JWD). In Vietnam, Nisbett and Ciochon (1993: 788) surmised that Rhesus macaque "lives in virtually all forest types except karst forest." Hill (1999), however, noted several records apparently from limestone forest of Ba Be National Park and perhaps other sites, but the basis for identification of these was not discussed.

Ecological overlap with northern pig-tailed macaque

Northern pig-tailed macaque has recently been found much further north in Lao PDR than suggested by records available to Fooden (1982). It occupies the Mekong plain north to at least Muang Sangthong, Vientiane municipality (Duckworth 1996) and even the lower hills in two northern areas supporting Assamese macaques, Nam Kading and Nam Pouy NPAs (Boonratana 1997; Evans et al. 2000). Persistent reports, but based only upon village information, suggest that pig-tailed macaque may occur north even to Louangnamtha province (Tizard et al. 1997; Johnson et al. 2003; Hamada et al. 2007) and while observations of two captives (in Oudomxai and Louangnamtha provinces; Hamada et al. 2007) provide some support for this, there is yet no direct field verification. Suitable, albeit generally rather small, lowland areas for pig-tailed macaque occur even into the northernmost province, Phongsali (for example, around Ban Muangyo; Fuchs et al. 2007). Such areas have been poorly surveyed for mammals. They are heavily settled and hunting levels are very high, so the pre-exploitation relative distribution of Assamese and pigtailed macagues in northern Lao may never be determined.

There are too few records with precise altitudes to assert the degree of altitudinal overlap between these two species in hill evergreen forest: available Lao observations fit Fooden's hypothesis that Assamese generally lives higher than pigtailed, although the two have been seen in several areas in similar habitat and altitude: on the Nakai plateau (only one Assamese macaque record, many pig-tailed; Evans et al. 2000; Dersu 2008; Appendix 2) and in Phou Xang He NPA (where both species were seen on the same day and in the same valley in the Phou Hinho sector (RJT); and, to some extent, in Nam Kading NPA (where a group of pig-tailed was recorded in the lower Nam An valley at 300 m, well below the records of Assamese) and at the foot of the Bolaven slope in Dong Hua Sao NPA (with the pig-tailed macaque record on the adjoining plains; RJT). In and around the main karst areas, however, there is coarse overlap but Assamese macaque has not been recorded far off karst whilst pig-tailed has been found only very rarely on it. There were two pig-tailed macaque records explicitly from karst in Hin Namno NPA in 1998 (Walston and Vinton 1999; but see caution above); at Kouan Houy, Phou

Hinpoun NPA, during 1–5 April 1998, a troop of about 17 pigtailed macaques was seen on sparsely vegetated karst cliffs, where Assamese macaques were also recorded, but in different portions of the cliffs (Steinmetz 1998b); and in extensive karst north of Phou Hinpoun NPA, 2 km from Ban Nahin at the plain's edge ($c.18^{\circ}11'N$, $104^{\circ}29'E$), J. Eaton ($in \ litt. \ 2011$) saw a lone male pig-tailed macaque on 28 December 2009, and a female with young (at 150 m a.s.l.) on 26 January 2011.

Southern range margin in Lao PDR

The southernmost Lao record of Assamese macaque, in Dong Hua Sao NPA at 14°58'N, is similar to the southernmost published record globally, from Chongkrong, Thailand (of 14°41'N, 98°52'E), close to the Myanmar border (Fooden 1971; Groves 2001). Francis's (2008) generalized range map indicates presence slightly further south in Vietnam. This map stems from a discussion for the 'South-east Asian Mammal Databank' and no original data are available (C. M. Francis in litt. 2010); its boundaries may be predictive, not evidentiary. Fairly detailed and extensive primate surveys some way north of this boundary, in Quang Nam province, at latitudes similar to the Bolaven plateau, did not find Assamese macaque at all (Minh et al. 2005), and Nadler et al. (2007: 11), stating that "the distribution in Vietnam is not very clear yet", knew of no records south of Phong Nha-Ke Bang NP (c.17°30'N). Although Fooden (1982) had detailed the 1931 Bolaven record, various key sources persist in confining the Lao distribution to the north of the country (for example, Corbet and Hill 1992; Rowe 1996; Brandon-Jones et al. 2004; Nadler et al. 2007).

National conservation status

The Assamese macaque ranges widely in Lao PDR, inhabits many protected areas, some of over 2,000 km² and some with extensive rugged terrain in which hunting is difficult, and persists even on small isolated karsts. Thus, it is unlikely to be imminently threatened in Lao PDR (see discussion in Timmins and Duckworth 1999; Steinmetz et al. 2011; Timmins et al. in press a, in press b). The paucity of records from the northern highlands could suggest widespread major declines. However, survey effort there was too low to detect many macaques by direct sighting (see above): recent camera-trapping in this area, in Nam Et-Phou Louey NPA, found bear macaque to be among the most commonly photographed mammals (Johnson et al. 2006). This NPA had more directobservation survey effort in the 1990s than any other northern highland NPA, yet there were no field sightings of bear macaque. Unlike bear macaque, Assamese macaque is not sufficiently ground-dwelling to be readily camera-trapped, forestalling independent triangulation of its abundance in the northern highlands. But, because much hunting in the northern highlands is by snaring, the more arboreal Assamese macaque should be less depleted than is bear macaque.

There is therefore no reason to expect major declines of Assamese macaques within the NPAs and other large, remote blocks of habitat in the short- to mid-term; but, as with all quarry species, the barely-restrained hunting of almost all mammals of domestic cat-size and larger, coupled with piece-meal and sometimes major (for example, new road) encroachment into remote forests, pose a severe long-term threat in the country. In sum, in a world of finite resources for conservation, Assamese macaque is of much lower in-country conservation priority than are the gibbons and most colobines (Timmins and Duckworth 1999; Duckworth 2008; Duckworth *et al.* 2010a; Coudrat *et al.* in press; Timmins *et al.* in press a, in press b).

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Appendix 1. Historical records of Assamese macaque Macaca assamensis from Lao PDR1.

Site name, location	Altitude(s) of collection	Date(s) of collection	
Beside Ban Muangngoy, 20°43'N, 102°41'E	Unknown ²	28 Nov. 1931	
Along the Nam Ou 80 km upstream of Ban Pak-Ou, 20°38'N, 102°39'E	Unknown	21 Jun. 1924	
Lo-Tiao, 20°20'N, 100°25'E	c.1,500 m	5 Jan. 1939	
Near the Mekong 110 km west-north-west of Vientiane, 18°28'N, 101°40'E	Unknown	4 Jul. 1924	
Ban Thateng ³ , Bolaven plateau, 15°26'N, 106°23'E	village: c.900 m	14 Dec. 1931	

Deuve (1972), in a purportedly comprehensive review of the mammals of Lao PDR, did not include the species; given his many other basic errors (see, for example, Timmins and Duckworth 1999) this should not be seen as indicating even scarcity in, still less absence from, Lao PDR at that time.

² "Half-way up the mountain" (Legendre 1936: 158).

³ Duckworth et al. (1999) spoke of multiple specimens from Thateng, but this seems to have been a slip; Fooden (1982) listed only one, and we know of no others.

Appendix 2. Recent (1992-early 2010) field records of Assamese macaque Macaca assamensis in non-karst habitats of Lao PDR.

Site name, location	Co-ordinates and altitude(s) of sighting	Date(s) of sighting	Reference(s)	Other notes
Northern highlands				
Nam Et-Phou Louey NPA	20°28'N, 103°14'E; 1,250 m	10 Apr. 2005; 15h08	A. Johnson in litt. 2011	Camera-trap record ¹
c.2 km north of Ban Tonglat-kao, Nam Ha NPA	20°58'N, 101°00'E; within 1,200–1,400 m	Feb. 1997	Tizard <i>et al.</i> 1997; P. Davidson <i>in litt</i> . 2010	
Central Nam Pouy NPA	18°34'N, 101°22'E; <i>c</i> .500 m	4 May 1997	Boonratana 1997; RB	Group of c.20
Annamites				
Nam Kading NPA	18°30"02"N, 104°05'37"E; 750 m	24 Dec. 2007 (14h57 & 15h04)	A. McWilliam in litt. 2010	Camera-trap record
Upper Nam An valley, Nam Kading NPA	18°18'N, 104°16'E; 745 m	14 Apr. 1995	Evans et al. 2000	
Upper ridge of the Nam An catchment, Nam Kading NPA	18°17'21"N, 104°14'51"E; 900 m	22 Apr. 1995	Evans et al. 2000; RJT	
North slope of Sayphou Ao, Nam Kading NPA	18°21'N, 104°27'E; <i>c</i> .550 m	2 May 1995	Evans et al. 2000; RJT	Provisional
Ridge south of the Nam Theun below the Nam Theun 2 dam-site	18°03'N, 104°57'E; 730 m	18 Feb. 1996	Dersu 2008; RJT	
North of Ban Nakadok, Nakai–Nam Theun NPA	18°11'N, 105°10'E; 750 & 850 m	[14] and 15 Jan. 1994	Evans et al. 2000	Two records, one provisional
Middle Nam Xot valley, Nakai–Nam Theun NPA	18°08'N, 105°15'E; <i>c.</i> 725 m	18 Jan. 1994	Evans et al. 2000	Provisional
Navang logging road, Nakai–Nam Theun NPA	<i>c</i> .18°01'N, 105°21'E; <i>c</i> .1,200 m	21 Apr. 1994	Evans et al. 2000	Provisional
Navang logging road, Nakai–Nam Theun NPA	17°58–18°02'N, 105°19–21E; across 1,000–1,300 m	24 Apr. – 14 May 1996	Duckworth 1998	Many records
Navang logging road, as above	Across 1,100-1,200 m	within 24 Feb. – 5 Mar. 1997	WCS 1997	Three records
Houay Morrow, Nakai-Nam Theun NPA	18°01'N, 105°21'E; 800 & 900 m	26-27 Feb. 1997	WCS 1997	Two records
Upper Nam On valley, Nakai–Nam Theun NPA	17°36'N, 105°41'E; <i>c</i> .780–880 m	Dec. 1995	W. G. Robichaud in litt. 1996	
Near Ban Kunaeh, Houay Manthon, Nakai-Nam Theun NPA	17°50'N, 105°35'E; <i>c</i> .820 m	26 Nov. 1998	Robichaud & Stuart 1999; W. G. Robichaud <i>in litt</i> . 2010	
Between Thong Khouang and Ban Nameo, Nakai–Nam Theun NPA	17°48'N, 105°32'E; 750 m	12 Dec. 1998	Robichaud & Stuart 1999; W. G. Robichaud <i>in litt</i> . 2010	
Nam Phao, Nakai-Nam Theun NPA	18°22'N, 105°10'E; 900 m	within 20-22 Mar. 1997	WCS 1997	Provisional
Phou Chomvoy, Nam Theun Extension pNPA	18°25'N, 105°03'E; 1,000 m	within 28 Mar. – 3 Apr. 1997	WCS 1997	Provisional
Tributary of the upper Nam Tang, Nam Theun Extension pNPA	18°34'N, 105°06'E; <i>c</i> .750 m	8 Jun. 1998	Robichaud & Stuart 1999; W. G. Robichaud <i>in litt</i> . 2010	
Tributary of the Nam Ta, Nam Theun Extension pNPA	18°34'N, 105°00'E; 550 m	31 May 1998	Robichaud & Stuart 1999; W. G. Robichaud <i>in litt</i> . 2010	Provisional
Nakai plateau	17°50'37"N, 105°11'26"E; 560 m	6 Feb. 2010	RJT	In mixed pine and semi-evergreen for- est on gentle terrain
Phou Hinho, Phou Xang He NPA	16°48'N, 105°57'E within 200–400 m	15 Apr. 1993	Duckworth et al. 1994, RJT	Provisional
Western slope of Phou Leng, Xe Sap NPA	16°02'N, 106°44'E; 800 m	within 15–20 Mar. 1999	Steinmetz et al. 1999	Provisional
Bolaven slope near Ban Houayton, Dong Hua Sao NPA	14°58'N, 106°10'E; <i>c</i> .400 m	11 Jul. 1993	Duckworth et al. 1994, RJT	

All records are direct sightings except where stated.

NPA = National Protected Area; pNPA = proposed National Protected Area.

¹Johnson *et al.* (2006) referred to Assamese macaque being camera-trapped in this NPA in 2003–2004, but re-examination of the photographs by RJT, JWD and A. Johnson found that the record in fact probably is of Rhesus macaque M. mulatta (as had been earlier indicated in Johnson et al. 2004).