Rodent outbreaks in the uplands of Laos: analysis of historical patterns and the identity of *nuu khii*

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Abstract. Rodent outbreaks in the uplands of Lao PDR (Laos) are understood by traditional farmers to be triggered by the episodic and synchronised flowering and seeding of certain bamboo species. Historical data from 24 districts spread across four provinces indicate that these outbreaks have been a feature of the upland agricultural environment for at least 50 years. Although many outbreaks appear to be fairly local in scale, records from Luang Prabang and Oudomxay provinces appear to document at least one widespread and prolonged outbreak, over the period 1988–1993. Somewhat surprisingly, there is no suggestion that rodent 'outbreaks' have become more frequent in recent times, contrary to widespread reports that the level of chronic rodent damage to crops has increased over the last decade. This apparent 'uncoupling' of trends in rodent outbreaks and agricultural crop losses adds weight to the traditional perception that the outbreak events owe their origin to factors outside of the agricultural systems.

A variety of rodent species are probably involved in the outbreak events. The identity of the ethnotaxon *nuu khii*, literally the 'rat of bamboo flowers', remains somewhat enigmatic. In some areas *nuu khii* may refer to one or more species of primarily forest-dwelling rat. However, in other areas, this term appears to describe an ecological phenomenon, namely the eruptive increase of forest rodent populations, with subsequent outpouring into adjacent agricultural landscapes.

The historical records do not help identify the cause of the rodent outbreaks. The pattern of outbreaks shows no clear association with generalised El Niño Southern Oscillation cycles, and with the exception of one geographically widespread outbreak in 1988–1993, there is little to suggest a regional climatic influence of any kind. The traditional belief that rodent outbreaks occur in response to bamboo flowering events is plausible in terms of the general biology of Southeast Asian bamboos, but the historical data do not allow for any direct test of this proposition. Much more information is required on the identity, distribution and phenology of Lao bamboo species, and on the impact of mast-seeding events on small mammal communities in the Lao uplands, before this interesting and economically important ecological phenomenon can be properly assessed.

Introduction

Across much of South and Southeast Asia, episodic rodent outbreaks in upland habitats are understood by traditional farmers to be triggered by the episodic and synchronised flowering and seeding of bamboos (Parry 1931; Janzen 1976; Chauhan and Saxena 1985; Rana 1994; Singleton and Petch 1994; Schiller et al. 1999). This process, otherwise known as bamboo 'masting', involves the production, usually over a period of one or two years, of large quantities of highly nutritious seed, which is believed to trigger explosive increases in rodent populations within the bamboo forest habitat. Following depletion of the bamboo seed-fall, mass emigration of rodents into adjacent agricultural habitats is claimed, leading in some cases to heavy crop losses and even famine (Singleton and Petch 1994; Nag 1999; Schiller et al. 1999).

Although similar connections have been made between bamboo masting and rodent outbreaks in other subtropical regions, including Japan (Numata 1970), South America (reviewed by Jaksic and Lima 2002) and Madagascar (Rakatomanana 1966), to date there has been no detailed study of this important ecological phenomenon. However, at a more a general level, the potential role of mast-fruiting or mast-seeding in driving episodic rodent outbreaks is abundantly demonstrated by examples from deciduous forests in North America (Wolff 1996; McShea 2000) and from cool–temperate forests in New Zealand (King 1983; O'Donnell and Phillipson 1996).

In various parts of Lao PDR (Laos), the rainfed upland ecosystem still plays a predominant role in meeting the food requirements of many ethnic groups. In the 2000 production year, upland rice cultivation accounted for approximately 12% of total production and 21% of the total area under rice cultivation (Lao PDR Ministry of Agriculture and Forestry records). Most upland rice cultivation is still based on the use of 'slash and burn', shifting cultivation systems. The productivity of the upland systems of production is generally in decline and problems associated with upland cultivation are on the increase (Schiller et al.1999; Roder 2001). Rodent damage and associated grain loss are cited by upland farmers as being second only to weeds as the most significant production constraints of the uplands. The damage attributed to rodents is a chronic annual problem in most of the Lao uplands. However, the severity of the problem varies from year to year and between localities.

The occurrence of explosive rodent outbreaks in the uplands of Laos was reported by Singleton and Petch (1994) and Schiller et al. (1999), based on information obtained during interviews with farmers and agricultural officers, and on the returns from rat bounty systems. Schiller et al. (1999) noted that rodent outbreaks occur at "irregular intervals" but they did not speculate on the frequency of such events. Nor did they identify the outbreaking rodent species, known locally as *nuu khii* (literally 'rat of bamboo flower'). Singleton and Petch (1994) suggested that the outbreaks might involve both *Rattus argentiventer* and a species of *Mus*, however this opinion was based on farmers' descriptions rather than direct observation of specimens.

In this paper, we present the results of historical investigations into rodent outbreaks in four upland provinces of Laos. The study area is characterised by shifting cultivation systems that produce a mosaic landscape of gardens, remnant forest and regrowth habitats (Roder 2001). We also shed new light on the identity of *nuu khii*, based on voucher collections made between 1998–2001.

Although rodent outbreaks have been noted for at least 50 years, the reasons for these outbreaks are not adequately known. To gain a better understanding of the physical and biotic factors that regulate rodent population cycles and their impact on crop production systems, the analysis of historical records of rodent population fluctuations is essential.

Materials and methods

Our main body of historical information comes from five provinces: four of these provinces (Luang Prabang, Oudomxay, Houaphanh and Sayabouly) are in the northern agricultural region, while one (Sekong) is in the south-east of the country (southern agricultural region). Each of the provinces is unique in respect of climatic and/or agronomic factors. Annual rainfall is highest in Sekong (>2000 mm) and lowest in parts of Luang Prabang and Sayabouly (<1440 mm) (Sisophanthong and Taillard 2000). Houaphanh is generally at a higher elevation than the other provinces and is considerably colder in the winter months than the other provinces. The 'summer' temperatures in Sekong are several degrees higher than in the more northerly provinces. Among the five provinces, the intensity of upland shifting cultivation is highest in Luang Prabang and Oudomxay (Sisophanthong and Taillard 2000).

In Luang Prabang, Oudomxay, Houaphanh and Sekong, information was obtained from four to eight districts. The sources of information accessed were: (1) documentary records held by the provincial offices of the Ministry of Agriculture and Forestry; (2) interviews with current and former staff of these offices; and (3) interviews with farmers. In Sayabouly, information was gathered exclusively from farmer interviews.

Information was sought on: the year and season of outbreaks; the rodent species involved and their approximate density; the geographical extent of outbreaks within the district; the crops affected and estimates of crop losses; and annual rainfall. Not all classes of information were obtained in all provinces or districts and the time period covered by the records also varies from 15 years (Sekong province) to 50 years (Luang Prabang and Houaphanh provinces).

Estimates of crop losses are based on reported cropping areas and yields from particular districts. Not all of the yield loss is necessarily due to rodent damage, which may be compounded by other factors. On the other hand, yield loss estimates typically will not register 'foregone' loss where farmers fail to plant crops in anticipation of their complete destruction by rodent pests. In analysing the historical data, outbreaks that occurred in consecutive years were treated as a single, extended event. Estimates of crop losses during these extended outbreaks support this interpretation (see Results and Discussion).

Rodent specimens were collected between 1998–2002 during the course of regular trapping programs in various agricultural and natural habitats in each of Luang Prabang, Oudomxay, Houaphanh and Sekong provinces. A smaller collection of voucher specimens was made in Sayabouly province in 2002. The trapping results and associated voucher specimens provide a detailed picture of the rodent communities in each province and some information on the pattern of habitat use during 'non-outbreak' years (Khamouane et al., this volume). The occurrence of *nuu khii* outbreaks in Viengthong district of Houaphan province during 2001 provided an opportunity to collect voucher specimens directly referrable to this ethnotaxon.

Results and discussion

What constitutes an 'outbreak'?

The historical data provide a combined total of 155 'outbreak' years across all four provinces. Estimates of crop losses during outbreaks show an exceptionally wide range, from as low as 2% to a maximum of 90% (mean + sd = 55% ± 23.5%). The low crop losses associated with some 'outbreaks' are intriguing, but make sense if rodent outbreak events are distinguished from chronic crop losses.

Singleton and Petch (1994) and Schiller et al. (1999) both report that farmers in the upland environment typically sustain annual crop losses to rodent damage in the order of 5–15%. Our discussions with farmers in Luang Prabang, Sekong and Sayabouly provinces suggest that the level of 'chronic' damage to upland crops has increased in many areas over the last decade. Interestingly enough, farmers generally attribute this trend to changes in cropping systems, grain storage practices or residency patterns. Furthermore, they consistently distinguish this chronic loss from the 'outbreak' phenomenon, which they generally associate either with droughts or with bamboo flowering events (see below).

Crop losses during outbreaks are generally said to exceed the normal chronic levels, sometimes to the point of crop devastation and famine. However, under the scenario where outbreaks are identified on criteria other than the intensity of associated crop losses, it is conceivable that some recognised outbreaks did not cause significant crop losses. For example, this could occur in a situation where rodents disperse out of the forest habitat at a time when few crops are present in the upland fields.

Historical pattern of rodent outbreaks

Luang Prabang

Data were obtained from eight districts, spanning the period 1950–2000. The earliest reported outbreak was in 1958 in Chomamy district. The frequency of outbreaks in any single district has varied from a minimum of one in Chomamy district to a maximum of five in Luang Prabang district (mean + sd = 2.9 ± 1.3 per district, N = 23). Individual outbreaks have ranged in duration from 1–5 years (mean + sd = 2.0 ± 1.2 per district), with the period between outbreaks (including the time since the last recorded outbreak) ranging from 1–42 years (mean + sd = 8.5 ± 9.8 per district) with no indication of clustering within this spread. Examination of individual district records suggests possible inter-district variation in the degree of regularity of outbreaks. For example, in Gnoy district, the three outbreak events, with durations of 4, 2 and 5 years, respectively, are each separated by 'quiet' periods of 7–8 years (last one ended in 1993). In contrast, in Phonexay district, the four recorded events, each of 1–2 years duration, are separated by less regular periods of 14, 12 and 6 years, while in Luang Prabang district, five outbreaks, each occupying a single year, are separated by periods of 2, 13, 3 and 1 year.

The historical pattern of outbreaks within Luang Prabang province (Figure 1) shows several interesting features. The first is the strong cluster of reported outbreaks over the period 1989–1993, when all but one district experienced a rodent outbreak of between 1–5 years duration. The second is the presence of several extended gaps during which few outbreaks were reported, such as before 1961, between 1971–1989, and since 1993. Various factors may account for these gaps, including uneven reporting or recollection of events, and the general disruption of agriculture across much of Luang Prabang province during the war years. However, the last 20 years of records are almost certainly free of any such uncertainties.

Bamboo flowering is mentioned in connection with 16 of the 23 rodent outbreaks. Drought conditions are also mentioned in relation to 10 outbreaks, either alone (N = 3) or in combination with bamboo flowering, while rainy conditions are noted for one outbreak. Unfortunately, no information was available for bamboo flowering events or unusual rainfall during 'non-outbreak' years.

All but two of the 23 rodent outbreaks in Luang Prabang province are said to have occurred during the wet season; the exceptions are outbreaks that extended across the wet and dry seasons in Luang Prabang district in 1991 and in Nambark district in 1995. The strong association with the wet season through the greater part of the record may simply reflect the fact that, historically, little crop was grown in upland Laos through the dry season. Over the last decade, the area of valley floor paddy under irrigation has increased, thereby increasing the likelihood of crop damage during the dry season.

Estimates of crop losses during outbreak years range from 2–90% (mean + sd = 48 ± 31%). The low crop losses associated with some 'outbreaks' are intriguing, but make sense if outbreak events are being distinguished from chronic losses. Detailed discussions with farmers in Pak Ou district suggest that the level of 'chronic' damage to upland crops has increased over the last decade. Interestingly enough, they attribute this trend to changes in cropping systems, grain storage practices and residency.

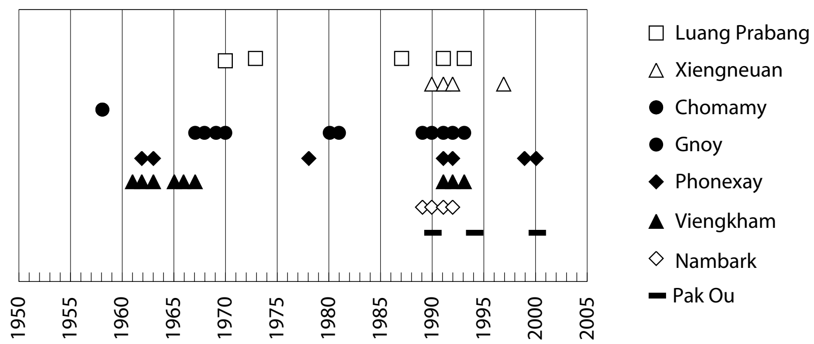

Figure 1. Historical pattern of rodent outbreaks in Luang Prabang province, by district.

Furthermore, they consistently distinguish this chronic damage from damage caused by the 'outbreak' phenomenon. Similar comments were obtained from farmers in Sekong and Sayabouly provinces.

Houaphanh

Information was obtained from eight districts. A total of 42 outbreaks were reported, the earliest dating from 1953 in Viengthong and Houameuang districts (Figure 2). The frequency of outbreaks per district ranges from 3–9 (mean + sd = 4.9 ± 1.4 per district). Most outbreaks occupy a single year, however there were three outbreaks of 2 years duration and three of 3 years duration (mean + sd = 1.2 ± 0.6 years). The mean interval between outbreaks, calculated across all districts, is 6.1 ± 4.3 years, with a suggestion of peaks at 4 years and 9–10 years. As in Luang Prabang province, there is considerable variation in the frequency and pattern of outbreaks between individual districts.

When the outbreak events are pooled across the entire province, the Houaphanh data show a weakly cyclic pattern with periods of more frequent and widespread outbreaks (e.g. 1953–1957, 1967–1974, 1981–1987) separated by periods of relative quiet. Other than in Xammneua district, there have been few records of outbreaks in Houaphanh province over the past decade, however this 'quiet' phase may have broken recently, with widespread outbreaks reported in late 2001, after this survey was completed.

All historical rodent outbreaks in Houaphan province occurred during the wet season, with the majority specified as occurring in September–October (again coinciding with the major cropping period). Bamboo flowering events are noted in relation to most outbreaks. Drought conditions are indicated for every outbreak in Viengthong district, but are not mentioned for outbreaks in any other districts. The estimates of associated crop damage range from 12% to 90% (mean + sd = 60.8 ± 19.0%).

Oudomxay

We have records covering the period 1975–2000 for each of four districts. For Beng and Xay districts, the information is limited to an estimate of damage where this value exceeds 10%. For La and Houn districts, there is some additional information on the timing of crop damage and bamboo flowering events. Rainfall data are available from a station in La district for the period 1987–2000.

Oudomxay province appears to have experienced a widespread and prolonged rodent outbreak spanning the period 1985–1995 (Figure 3). In all four districts, the highest levels of damage were reported in 1990, with reported crop losses of 40–70% during that year. The local rainfall records show that 1990 was a year of especially severe drought in Oudomxay, with dry conditions also in 1987 and 1992–93. However, higher than average rainfall fell in each of 1991 and 1994, hence any link between rainfall and rodent populations must be complex if indeed

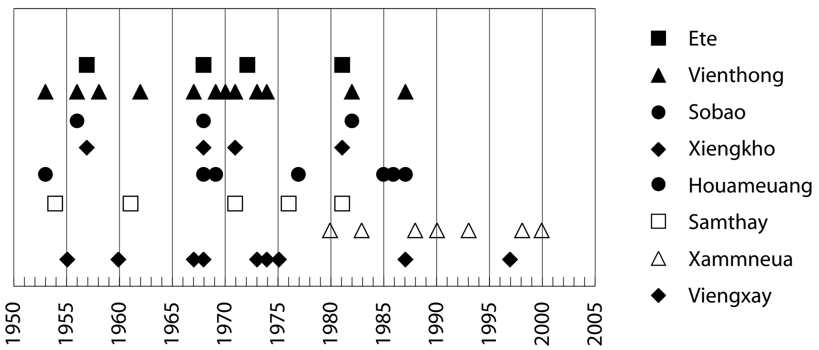

Figure 2. Historical pattern of rodent outbreaks in Houaphanh province, by district.

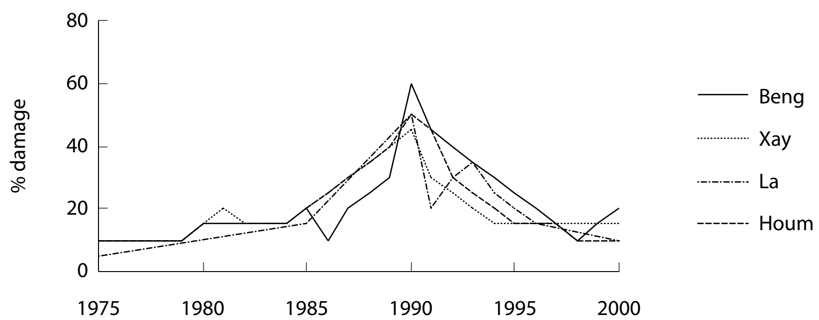

Figure 3. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Oudomxay province.

it exists at all. Bamboo flowering is not mentioned other than for the period 1975–77 in La district and for 1975–78 in Houm district. Interestingly enough, the period of most intense damage in Oudomxay province coincides with the 1989–1993 outbreak identified in nearly all districts of Luang Prabang province to the immediate east.

Sekong

Records are available for the period 1984–2000 from four districts; local rainfall data are available for each district for all or part of this period. The pattern of outbreaks appears to differ markedly between districts. In Duckchiang district, there have been rodent outbreaks almost every year since 1984, with extreme crop losses in the range of 60–75% (Figure 4). In contrast, the other districts appear to experience episodic outbreaks, typically lasting 1–3 years, but separated by 'quiet' periods of 1–2 years. Crop losses of 50–80% are reported during the outbreak periods. The regular cycle of outbreaks is most obvious in the data from Lamam district.

The Sekong rainfall data indicate that Kaleum and Lamam districts are much drier overall than Thateng or Duckchiang (Figure 5). Fluctuations in rainfall since 1984 show no obvious association with reported outbreaks or with the severity of crop damage. For example, in Thatheng district, severe rodent damage occurred in both very wet years (e.g. 1991, 1995) and very dry years (e.g. 1989, 1996).

In all districts, the timing of rodent outbreaks has evidently changed during the period covered by the records, shifting from an exclusively wet-season phenomenon to one that spans both wet and dry seasons. This change evidently occurred at different times in different districts (i.e. 1993 in Lamam, 1995 in Thatheng, 1996 in Duckchiang, 1997 in Kaleum) and it is possible that it reflects the gradual increase in irrigated dry-season paddy over this period. Bamboo flowering events are not mentioned at all in the Sekong data set.

Sayabouly

A detailed historical survey was not undertaken in Sayabouly province. However, interviews with farmers in 2002 suggest that *nuu khii* outbreaks are qualitatively different from normal fluctuations in rodent communities within the village and field habitats. They are said to involve a different species of rodent that emanates from the forest habitat (located approximately 3–5 km away), and to occur episodically—the last one in 1993. A connection with bamboo flowering events in the forest habitat was mentioned, but our informants themselves had not observed an initial eruptive phase in the forest.

The identity of *nuu khii* and other rodents

Six different ethnotaxa are mentioned as being involved in outbreaks (Table 1). As reported by previous authors (Singleton and Petch 1994; Schiller et al. 1999), *nuu khii* is mentioned more often than any other ethnotaxon (53.8% of outbreaks), followed by *nuu ban* (34.4% of outbreaks). The ethnotaxon *nuu mone* (grey colour rat) was mentioned only in Houaphanh province. Many

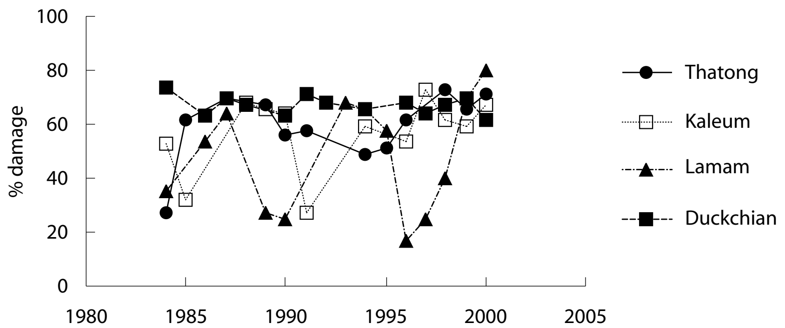

Figure 4. Recent pattern of crop damage attributed to rodent outbreaks in four districts of Sekong province.

Figure 5. Variation in annual rainfall in four districts of Sekong province.

outbreaks mention both *nuu khii* and *nuu ban* as jointly responsible for the crop damage.

Nuu ban is variously translated as 'house rat', 'field rat' or 'white-bellied rat'. Although Singleton and Petch (1994) tentatively identified this taxon as *Rattus argentiventer*, collections made in six provinces since 1998 suggest that *nuu ban* actually refers to one or more members of the *Rattus rattus* complex, which in Laos comprises the dominant species of village, garden and disturbed forest habitats (Aplin, Chesser and ten Have, this volume). To date, *Rattus argentiventer*, the true 'rice-field rat' of Southeast Asia, is recorded only from lowland habitat in Khammouan province (Francis 1999). The lesser rice-field rat (*Rattus losea*) also is recorded from Khammouan province (Francis 1999) and from one locality in Sekong province (Musser and Newcomb 1995), although it has not been encountered during the course of our fieldwork. Neither of these taxa is likely to be involved in the outbreak events discussed here. An interesting observation on *nuu ban* is that this taxon appears to be more frequently mentioned in 'outbreaks' over the last decade than during earlier times.

Three other ethnotaxa are mentioned either infrequently or on a local basis only. The name *nuu american* (literally 'foreign rat') is applied widely within Laos for *Bandicota indica* (in Sayabouly province this species is also called *nuu ngay*). This taxon was mentioned only twice in relation to outbreaks in Luang Prabang, and farmers in Pak Ou district further claim that this species does little damage compared with *nuu ban* or *nuu khii*. *Nuu mone* is mentioned only for outbreaks in Houaphanh province; this may be a local name for a member of the *R. rattus* complex. In Sayabouly province, a member of this complex was identified as *nuu puk*, further demonstrating the inter-regional diversity within the system of local names.

The identity of *nuu khii* remains enigmatic. In Sekong province, specimens of *Mus cervicolor* and juvenile *Rattus 'rattus'* were both identified as *nuu khii*, in keeping with earlier suggestions that this ethnotaxon might refer to a true mouse. However, farmers in Pak Ou district of Luang Prabang province claim that *nuu khii* is not a species of *Mus*, which they generally identify as *nuu sing*. They also distinguish *nuu khii* from *nuu waay* ('rattan' rat) which, from its description (as a red-backed, white-bellied forest rat), may include *Maxomys surifer*, one or more *Niviventer* species, and possibly also *Chiromyscus chiropus*. In Sayabouly province, farmers were adamant that *nuu khii* is different from *nuu puk* (*R. 'rattus'*). They also claimed that, other than during outbreak events, *nuu khii* is not found in the agricultural landscape. Instead, it is a forest rat that periodically emerges from the forest as a 'rat army' that moves through the agricultural landscape destroying any crops that it encounters. Their detailed description of *nuu khii*—as a short-furred, greyish rat, around 20 cm in body length, with a pure-white belly and a single-coloured tail about equal in length to the body—could fit equally well with several possible candidates, including a species of *Niviventer* or possibly *Berylmys bedmorei*. To date, we have been unable to obtain a voucher specimen of *nuu khii* from Sayabouly for local and scientific identification.

Nuu khii outbreaks in several districts of Houaphan province in 2001 did finally provide an opportunity to obtain voucher specimens for this ethnotaxon. The resultant sample, identified collectively as *nuu khii*, includes a variety of rat species including two different members of the *R. rattus* complex. At least in Houaphanh province, the taxon *nuu khii* thus appears to be an ecological category, perhaps signifying that a particular rodent outbreak is due to conditions or circumstances within the forest habitat rather than the agricultural landscape. However, at a broader scale, these varied results suggest that the term *nuu khii* may be used in different ways across Laos.

Rodent outbreaks and El Niño

The historical information from Laos points to considerable regional heterogeneity in the pattern of rodent outbreaks, even within a single province. However, there is also some evidence for broad-scale synchrony of outbreaks, especially within and between the northern provinces of Luang Prabang and Oudomxay.

The question of what environmental factors might be driving these events is an interesting one from an ecological perspective and a critically important one if resultant crop damage is to be mitigated. The two factors that obviously warrant early consideration are large-scale climatic perturbations and bamboo masting events.

Laos falls within the geographical area influenced by the El Niño Southern Oscillation (ENSO) (Holmgren et al. 2001). El Niño events, caused by anomalously warm sea surface temperatures in the equatorial eastern Pacific, typically occur once every 3–6 years, with widespread and

Table 1. Frequency of mentions of various ethnotaxa in reported outbreaks.

Province	*nuu khii*	*nuu ban*	*nuu american*	*nuu na*	*nuu mone*	*nuu tongkao*	Total
Luang Prabang	36	7	2	1			46
Houaphanh	28	11			8		47
Sekong	20	37		3		3	63
Oudomxay	2			2			4
All combined	86	55	2	6	8	3	160

diverse consequences on both natural and agricultural ecosystems (Meserve et al. 1995; Lima et al. 1999; Zubair 2002). Across Southeast Asia, the impact of El Niño events varies both regionally (Holmgren et al. 2001) and in accordance with the time of onset of the oscillation (Kane 1999). In Laos, the impact appears to be especially variable (Hompangna et al. 2000), although in recent times it has more often led to widespread drought (e.g. El Niño of 1987, 1991–1992, 1997) than to flooding (e.g. El Niño of 1982).

Over the 50-year period covered by the rodent outbreak data, particularly strong El Niño events (as estimated from monthly values of the Southern Oscillation Index) occurred in 1953, 1965, 1972, 1977, 1982–83, 1986, 1991–92, 1994 and 1997–98 (Yue 2001). However, data on the impact of these events across Southeast Asia (Kane 1999) and in Laos specifically (Hompangna et al. 2000) suggest that widespread severe droughts were experienced only in 1965 and 1972, with widespread flooding in 1953 and 1983. The El Niño event of 1991–92 had variable effects in Laos, with drought in the northern provinces but above normal precipitation and some flooding in the south (Hompangna et al. 2000). The 1997–98 El Niño event, rated on some measures as the strongest on record (McPhaden 1999), resulted in widespread drought across Laos in 1998 and a marked increase in forest fires during the dry season of 1998–99 (Hompangna et al. 2000).

The geographically widespread and prolonged nature of the rodent outbreaks in Luang Prabang and Oudomxay provinces in 1989–94 suggests the possibility of some underlying climatic control. These outbreaks followed directly on the El Niño of 1987–88 and overlapped the El Niño of 1991–92. However, as noted earlier, local rainfall data covering this period show complex inter-annual variations, and suggest a need for caution in any interpretation. At a larger scale, the long-term rodent outbreak records from Luang Prabang and Houaphanh provinces do not show any clear pattern of association with El Niño events. While this does not rule out the possibility that climatic factors were behind some or all of the outbreaks, it does suggest that any linkage is likely to be complex. Lima et al. (1999, 2001) found that both a delayed density-dependent response and predator–prey relations mediate the effect of ENSO-related rainfall variations in causing rodent outbreaks in western South America. In the agricultural landscape of the Lao uplands, additional complexity might be anticipated, related to the impact of climatic events on the diverse cropping systems.

Rodent outbreaks and bamboo masting

The wider Asian region supports a high diversity of bamboos, probably around 140 species in all. Mast-seeding is common but not ubiquitous within the group, and it is generally more prevalent in areas with strongly seasonal climates (Janzen 1976; Soderstrom and Calderón 1979). Among bamboos, mast-seeding appears to be controlled by internal, genetically determined factors, such that individuals flower and seed after a certain number of years of growth (Janzen 1976). This is unusual among mast-seeding plants, which more typically do so in response to environmental triggers (Kelly 1994). Bamboos are unusual in two further respects. Most species are semelparous, which means that they usually die after setting seed, and many have a very long period of vegetative growth before seeding, with recorded intermasts of 3–120 years (Janzen 1976). Most Asian mast-seeding bamboos have intermast periods in the order of 15–60 years.

The majority of Southeast Asian bamboos flower at the end of the wet season such that the seeds ripen and fall over the dry season. Many species flower profusely and produce copious quantities of seed. Individual seeds range in size from rice kernel- to pear-sized, with total productivity estimates for two Indian species of around 1 kg of seed/m^2 (*Bambusa arundinacea*; Gadgil and Prasad 1984) and 3.6 kg/m^2 (*Dendrocalamus strictus*; Janzen 1976, p. 355). The seed itself has nutrient qualities slightly greater than rice or wheat, and appears to be unprotected by toxins (Janzen 1976). Apart from rats, many other groups of animals are reported to feed on bamboo seed in the Asian context, including many birds (jungle fowl, pheasants, pigeons, parrots), ungulates (cervids and bovids) and rhinoceros (summarised by Janzen 1976, pp. 354–363). Large congregations of feeding birds are reported, but there are no detailed ecological studies of such events.

Although all mast-seeding bamboos by definition display some degree of synchrony in flowering and seeding, the duration and geographical scale of the 'events' vary considerably. In many species, seeding occurs synchronously at the level of an individual clump or closely related group of clumps, but with no overall geographic consistency. Large-scale synchrony is much less common. In India, for example, 70 of 72 bamboo species are mast-seeders but only eight are recorded as flowering synchronously at the district level or wider (Keeley and Bond 1999). However, where widespread synchrony does occur, it can be on a staggering scale. Janzen (1976, p. 361) cites examples from India of mast-seeding across 1200 square miles for *Dendrocalamus strictus*, 6000 square miles for *Melocanna bambusoides* and "hundreds to thousands of square miles" for *Bambusa polymorpha*. Keeley and Bond (1999) suggest a typical scale for synchronous flowering of 102 to 103 hectares. Synchrony is, of course, only a relative concept, and it should be noted that the mast-flowering and mast-seeding process is usually spread over 2–5 years, even within the confines of a single clump (Janzen 1976; Gadgil and Prasad 1984). Fallen bamboo seeds typically germinate after the first rain and they display no special adaptation for dormancy; indeed, they appear to lose their viability (and presumably some of their nutritional value) after one or two months, even if kept dry (Janzen 1976).

Little specific information is available on the bamboos of Laos. Gressit (1970) listed five genera of Bambusacae as occurring in Laos (*Arundinaria*, *Bambusa*, *Cephalostachyum*, *Dendrocalamus* and *Oxytenanthera*).

Bamboos are conspicuous in many upland habitats, with large stands situated along watercourses and in many areas of former slash-and-burn activity. Roder et al. (1995) mentioned two species as important fallow species, *Bambusa tulda* and *Dendrocalamus brandisi*i, while Singleton and Petch (1994, Table 2.10) mentioned two species (*Bambusa tulda* and *Oxytenanthera parvifolia*) as specifically implicated in rodent outbreaks. The intermast period of *B. tulda* is given by Rana (1994; see also Singh et al. 1994 for identity of bamboo species) as 48–50 years and this species is further said to display widespread synchrony of mast-seeding. Species of *Dendrocalamus* typically have long intermast periods in the range 30–50+ years and this genus also includes species with large-scale synchronised masting. Interestingly enough, both of the major fallow bamboos are included by farmers among their suite of 'good' fallow plants (Roder et al. 1995, Table 4). Where bamboo is involved in garden fallow systems, short-term regeneration presumably occurs from rhizomes remaining within the ground after land preparation (Christanty et al. 1996). According to Janzen (1976), the cutting, burning or transplanting of a mast-seeding bamboo generally will not impact on its genetically determined flowering calender.

Conclusion

The traditional belief that rodent outbreaks occur in response to bamboo flowering events is clearly plausible in terms of the general biology of Southeast Asian bamboos. Bamboo masts—involving the episodic mass-production of an abundant, highly nutritious food resource—are an example of a 'pulsed resource' (*sensu* Ostfeld and Keesing 2000) and as such, may well underpin episodic outbreaks of vertebrate consumers, including rodents, either directly or through intermediate ecological linkages. Jaksic and Lima (2002), after reviewing the historical and ecological evidence of South American 'ratadas', also concluded that bamboo masting may be responsible for some of these events, especially in Brazil. However, as in Laos, the South American evidence is largely circumstantial. A detailed ecological study of a Lao *nuu khii* outbreak or a Brazilian 'ratada' in progress is sorely needed.

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