RESEARCH ARTICLE

Co-existence between Javan slow lorises (*Nycticebus javanicus*) and humans in a dynamic agroforestry landscape in West Java, Indonesia

K.A.I. Nekaris [1, 2*], S. Poindexter [1], K. D. Reinhardt [1], M. Sigaud[1], F. Cabana[1], W. Wirdateti [3], V. Nijman [1, 2]

1. Nocturnal Primate Research Group, Oxford Brookes University, Oxford, United Kingdom

2. Oxford Wildlife Trade Research Group, Oxford Brookes University, Oxford, United Kingdom

3. Zoological Division, Indonesian Institute of Sciences, Cibinong, Indonesia

For *International Journal of Primatology*

Total word count 8022

ABSTRACT

In a world increasingly dominated by human demand for agricultural products, we need to understand wildlife's ability to survive in agricultural environments. We studied the interaction between humans and Javan slow lorises (*Nycticebus javanicus)* in Cipaganti, Java, Indonesia. After its introduction in 2013, chayote (*Sechium edule)*, a gourd grown on bamboo lattice frames, became an important cash crop. To evaluate people's use of this crop and to measure the effect of this increase on slow loris behaviour, home ranges, and sleep sites, we conducted interviews with local farmers and analysed the above variables in relation to chayote expansion between 2011-2015. Interviews with farmers in 2011, 2013 and 2015 confirm the importance of chayote and of bamboo and slow lorises in their agricultural practises. In 2015 chayote frames covered 12% of land in Cipaganti, occupying 4% of slow loris home ranges, which marginally yet insignificantly increased in size with the increase in chayote. Slow lorises are arboreal and the bamboo frames increased connectivity within their ranges. Of the sleep sites we monitored from 2013-2016, 24 had disappeared, and 201 continued to be used by the slow lorises and processed by local people. The fast growth rate of bamboo, and the recognition of the value of bamboo by farmers, allow persistence of slow loris sleep sites. Overall introduction of chayote did not result in conflict between farmers and slow lorises, and once constructed the chayote bamboo frames proved to be beneficial for slow lorises.

KEY WORDS: agroforestry, conservation, ethnozoology, chayote, *Sechium edule*, sleep site, *Nycticebus javanicus*

INTRODUCTION

Preservation of high quality forest habitats is vital for the conservation of global biodiversity. Yet, in a world increasingly dominated by humans with their ever-growing demands for agricultural products, an understanding of wildlife's ability to survive and even thrive in agricultural environments is increasingly important (Bhagwat et al. 2008; Estrada et al. 2012; Stafford et al. 2016; Estrada et al. 2017). To meet this need, researchers have suggested new approaches to study biodiversity, integrating agricultural matrices into conservation planning for the preservation of rare species that also occur outside of pristine environments (Meijaard and Sheil 2008; Cassano et al. 2014). Farming systems that are intercropped by hedgerows or living fences of trees have often been regarded as vital contributors to alleviation of fragmentation (Michel et al. 2006). In Europe, where deforestation has been occurring for centuries, hedgerows are often the only habitat left for wildlife (Gelling et al. 2007), and have thus been well studied in the context of mammalian density, dispersal ability and behavioural ecology (Michel et al. 2007; Zhang and Usher 1991). Even for forest specialists, hedgerows have been shown to be important habitats, making up parts of forest dwelling animals' home ranges and as dispersal vectors (Schlinkert et al. 2016). For tropical mammals, such studies have lagged behind, but are now necessary as intact habitats disappear at an alarming rate.

Researchers often study tropical mammals, including primates, in 'pristine' habitats, rather than in disturbed, modified or anthropogenic habitats, with an idea that evolutionary adaptations can only be studied in such contexts (Hockings et al. 2015). Increasingly, however, the importance of anthropogenic habitats to primate ecology, conservation and evolution are recognized (Asensio et al. 2009, Estrada et al. 2017). For some species, agricultural landscapes may be beneficial not only to primates, but also to humans when primates control pests, pollinate flowers, or simply live peaceably without damaging their crops (Estrada 2006, Williams-Guillén et al. 2006). Although such interactions are not always amicable, primates can show remarkable behavioural flexibility, including dietary and habitat switching, and changes in polyspecific interactions (Tisovec 2014; Moore et al. 2010; Morrogh-Bernard 2014; Nowak and Lee 2013), making the study of the long-term sustainability of such systems important for primate conservation.

Agroforestry systems, areas in which trees or shrubs are grown around or among crops or pastureland, are one type of landscape where humans and primates may come together (Estrada et al. 2012). Considering mainly diurnal primates, Estrada et al. (2012) defined a number of ways primates can be useful to these systems, benefits also offered by a number of nocturnal primates. Researchers have recorded the pollination of agricultural plants by nocturnal primates (Javan slow lorises *Nycticebus javanicus* in Java, greater slow loris *N. coucang* in Malaysia) (Nekaris 2014; Wiens et al. 2006). Insect consumption, which is also likely to include agricultural pests, has been observed in agroecosystems among Javan slow loris in Java (Rode-Margono et al. 2015), Mysore slender loris (*Loris lydekkerianus lydekkerianus*) in India (Nekaris and Rasmussen 2003; Kumara et al. 2016), Milne-Edward's potto (*Perodicticus edwardsi*) in Cameroon (Pimley et al. 2006), and by Dian's tarsier (*Tarsius dianae*) in Sulawesi (Merker et al. 2005).

Being able to survive in human-modified landscapes is not enough; a tolerance between humans and primates must exist, in that humans do not trap primates for food or pets, or harm them over conflicts for food resources (Lee 2010). Mantled howler monkeys (*Alouatta palliata*) can feed and persist well in shade coffee plantations if left undisturbed by humans, including capturing them for the pet trade (Williams-Guillén et al., 2006). Additional management by humans may also be required, such as increasing connectivity between planted trees to aid in travel or predator avoidance, such as was observed in Brazil's cacao (*Theobroma cacao*) agroforests for Wied's marmosets (*Callithrix kuhlii*) and golden-headed lion tamarins (*Leontopithecus chrysomelas*) (Tisovec et al. 2014). Several macaque (*Macaca* spp) populations also can persist alongside humans, where being caught for pets or for the biomedical industry is a looming threat (e.g. Shepherd 2010).

The island of Java, Indonesia, is one of the most densely populated areas on earth. Java is largely deforested and most of the remaining 10% forest covers (parts of) the numerous volcanoes on the island (Whitten et al. 1996). Forest has been replaced by a mosaic of cities and villages, agricultural land, cash-crop plantations, and forest plantations (e.g., teak *Tectona grandis*, Sumatran pine *Pinus merkusii*, rubber *Hevea brasiliensis*) (Nijman 2013). About 17% of the agricultural land on Java consists of home gardens and agroforest, whose forest-like structure more or less mimic natural forest (Whitten et al. 1996), thus greatly increasing connectivity for many species.

Javan slow lorises, nocturnal primates endemic to Java, are characterized by fully arboreal slow climbing locomotion (Nekaris 2014). As such, one would expect them to be particularly vulnerable to habitat fragmentation where movement on the ground is often a requirement (c.f. Mortelliti et al. 2013; Vaughan et al. 2007). Slow lorises in general, however, are adapted to life at forest edges where increased sunlight creates a dense network of branches (Chivers 1980). Studies in the village of Cipaganti, Java, an agroforest ecosystem with a particularly high density of this Critically Endangered primate, show that slow lorises enter a sleep site at dawn, where they remain until dusk. As with most other primates (Anderson 1998), slow lorises do not use nests but instead sleep on a branch or tangle of branches, curled in a ball or huddled against group mates, within their chosen sleeping tree (Nekaris 2003). Such sleep sites are generally dense and have been hypothesised to protect them from extreme temperatures and predators (Nekaris 2014). Being territorial, the sleep sites of a slow loris group (male-female pair and offspring) fall exclusively within their own home range. Bamboo stands comprise 96% of sleep sites for Javan slow lorises in Cipaganti, as well as substrates for feeding and avoiding ground movement (Nekaris 2014). Bamboo stands are used (and re-used) as sleep sites daily by slow lorises. Typically, 20 to 40 bamboo sleep sites are present in each slow loris' home range (first author, unpubl. data).

Cipaganti is characterized by shifts in agriculture, with the types of crops grown depending on local economic trends. For example in 2012, when tomatoes (*Solanum lycopersicum*) were economically valuable, farmers heavily planted this crop. Similarly, in 2013, farmers began growing a gourd, chayote (*Sechium edule*), and by 2015 it became the crop of choice. Chayote, locally known as *labu*, relies on a network of bamboo frames in order to grow (Fig. 1). These frames are erected at ~1.6 m in height and can be up to 1 ha in size, and cover what would have been open ground with a network of chayote vines growing on the frames. Due to the increasing interest by farmers in planting chayote, we noted an accelerated rate of cutting of bamboo, possibly impeding on the survival of the Javan slow lorises. Here, we examine the impact of this new agricultural development on the behaviour of slow lorises by addressing five questions. (1) Did farmers' perceptions of slow lorises, slow lorises perceived roles as consumer of agricultural pests and the importance of chayote to farmers change over the study period? We assessed this through informal interviews with farmers over the period 2011-2015. (2) Did the amount of land planted with chayote change, and did chayote frames make up a significant proportion of slow loris home ranges? We assessed this by measuring the proportion of land allocated to growing chayote in 2014 and 2015, as well as measuring the proportion of the slow loris home range comprised of chayote, also for 2014 and 2015. (3) Did slow loris home range sizes change or move position? We assessed this for 2014 and 2015 through direct observations. (4) How did slow lorises behave in and around chayote frames? We assessed this through behavioural observations in 2012 through 2016. (5) Did cutting bamboo for chayote affect availability of slow loris bamboo sleep sites? We assessed this in 2016 by measuring the presence and intactness of bamboo sleep sites at differing altitudes that had been used in the period 2013 to 2015.

METHODS

Ethical Note

We conducted all animal research in adherence with RISTEK (Indonesian Ministry of Science and Technology), as well as ethical guidelines provided by the Association for the Study of Animal Behaviour; Oxford Brookes University Animal Ethics Sub-committee granted our research approval. For the interviews we followed the ethical guidelines proposed by the Association of Social Anthropologists of the UK and Commonwealth and that the University Research Ethics Committee of Oxford Brookes University approved.

Study site and its changing farming practices

This study forms part of a long-term community conservation project to protect Asia's slow lorises and other imperilled nocturnal animals via ecology, education, and empowerment (Nekaris 2016). We conducted the study in an area of ~60 ha at the outskirts of the village of Cipaganti, Cisurupan, Garut Regency, West Java, Indonesia (7°16'44.30 "S, 107°46'7.80 "E, 1200 m asl) (Fig. 2). Cipaganti is home to about 3,000 people, living at a density of 135 people km^{-2} (Nekaris 2016). The village is located at 1,345 m asl on Gunung Puntang, a mountain that is a part of the Java-Bali Montane Rain Forests ecoregion. The climate is everwet with a mean annual precipitation exceeding 2,500 mm. The habitat around

Cipaganti is a mosaic of traditional gardens, where local farmers practice an annual perennial rotating crop system. This system consists of a variety of crop formations, with tall trees planted in rows along farm property boundaries, or interspersed between crop types (Reinhardt et al., 2016). In our study site, slow lorises heavily use certain plants including string bamboo (*Gigantochloa atter*), clumping bamboo (*G. pseudoarundinacea*), giant bamboo (*Dendrocalamus asper*), cajeput tree (*Malaleuca leucadendra*), red fairy duster (*Calliandra calothyrsus*), green wattle (*Acacia decurrens*), avocado (*Persea americana*) and Indonesian mahogany (*Toona sureni*) (Rode-Margono et al. 2014). Within the village of Cipaganti, agricultural production provides the main source of household income, yielding crops such as tea (*Camellia sinensis*), coffee (*Coffea robusta*), chayote (*Sechium edule*), carrot (*Daucus carota*), white cabbage (*Pieris brassicae*), tomato (*Solanum lycopersicum*), cassava (*Manihot esculenta*) and potato (*Solanum tuberosum*).

Chayote is a medium- to high-altitude crop (300 to 2,000 m asl) that requires a high relative humidity of around 80 to 85%, high annual precipitation of at least 1,500 without a marked dry season, and 12 hours of daylight to initiate flowering. The temperature should be between 13 and 21°C; temperatures below 13°C damage small and unripe fruits whereas temperature above 28°C leads to excessive growth, loss of flowers and unripe fruit, and ultimately reduced production (Saade 1996). Cipaganti matches these conditions extremely well. The Garut Regency in which Cipaganti is situated is an important grower of chayote, both in absolute and relative terms, and the area set aside for growing the crop in Garut has increased from 188 ha in 2012 (22% of the provincial total) to 360 ha in 2015 (33% of the provincial total). Production in 2015 was 14,499 t a year (c.f. Morton 1981). If both the official government figures and the estimates from the farmers in Cipaganti are correct then the wider Cipaganti area (which stretches beyond our study area) is responsible for some 60% of the regency's chayote production, suggesting that this crop will at least be around for the foreseeable future with a continuing impact on slow lorises.

Interviews with Informants

In June 2011, June 2013, December 2015 and June 2016 we held informal interviews (Newing 2011) with opportunistically selected key informants with farms situated within the home ranges of collared slow lorises (six informants in 2011, 16 in 2013, and 17 in 2015). Most informants lived in the village and were long-time residents (and typically born here or had moved into the area during childhood); in addition we interviewed five informants from neighbouring villages. In 2011 and 2013 the conversations focussed on the importance of slow lorises to the village, both from a cultural, natural and economic perspective. Given that chayote was not of particular importance at that time, farmers did not single out this crop but discussed it in the context of general agricultural crops. In 2015 the topic of discussion was similar to that in 2011 and 2013 but now much of it centred on chayote; given the dominant role of chayote in the agricultural landscape and the village economy, informants initiated discussions on this topic.

We held informal interviews in Bahasa Indonesia, the national language that is very widely spoken on Java (Sneddon 2004), repeating key concepts in Bahasa Sunda, the regional language spoken in this part of the island. Informal interviews were open, allowing informants to talk freely about slow lorises, their significance in culture or the beliefs surrounding them, and their role in the agricultural system. To ensure independence of data, we interviewed informants individually; other members of the community sometimes were present, but we used only the responses of the informant in analysis. At the end of each interview, we repeated key points to ascertain whether we captured the essence of the informant's opinions/expressions correctly. Informants did not receive gifts or money for their participation.

We asked informants to share any knowledge they had of slow lorises, touching upon any topic they felt to be relevant, without any constraint placed upon them by us (Bernard 2011; Puri 2011). We converted these conversations into freelists, from which we extracted the frequency of occurrence for each item (i.e. what proportion of informants mentioned topics such as 'slow lorises are useful for pest control', 'bamboo', or 'chayote') and the rank for each item (i.e. were they mentioned early on or at the very end of the interview, on a scale from 1 to 4) (Puri 2011). This procedure allowed us to check whether these topics were locally salient or meaningful. Salience was quantified by calculating Smith's *S* ($S = ((L - R_j + 1)/L)/N$, where L is the number of distinct items listed by the informants, R_j is the rank of item J in the list, and N is the number of lists / informants in the sample). Smith's *S* ranges from 0 to 1, with topics having values close to 1 being the ones that were mentioned by most informants early on in the conversation, and topics having values close to 0 being the ones that few informants mentioned, and if so often late in the conversation (Puri 2011).

Slow loris behavioural observations

To examine the presence of chayote in slow loris home ranges, we surveyed the study site to locate each chayote frame, measuring their perimeters and monitoring change in their presence from January 2014 to May 2015. To examine the behaviour of slow lorises in relation to chayote frames, we analysed behavioural data collected on collared slow lorises from the first time we saw them enter a chayote frame in June 2014 until June 2016. Because Javan slow lorises live in stable uni-male uni-female pairs with almost 100% range overlap and share sleep sites (Nekaris 2014), we examined the impact of chayote frames on social groups rather than individuals. We focus on adult individuals belonging to eight focal uni-male uni-female social pairs (Table 1). After catching the slow lorises by hand, we equipped them with 19 g VHF collars (PIP3, Biotrack, Wareham, United Kingdom). With the assistance of local field trackers, we located collared individuals using an antenna (Lintec flexible, Biotrack, Wareham, United Kingdom) and a receiver (Sika receiver, Biotrack, Wareham, United Kingdom), and recorded their location every 15 minutes using a handheld GPS unit (GPS62s, Garmin International, Olathe, USA). For direct observations we used head torches (HL17 super spot, Clulite, Petersfield, UK) fitted with a red filter. To observe the behaviour of slow lorises in chayote, we followed slow lorises for 3199 hours between 17:00-05:00 hrs, from January 2014 to December 2015 (a mean of 13 $\pm$ 7 nights per month). We used all occurrences sampling to record each instance one of the 16 focal lorises entered chayote using a modified version of the Rode-Margono et al. (2014) behavioural ethogram. Chayote frames are very dense and often when slow lorises enter these frames they are out of sight until they re-emerge into a tree or bamboo. To see if slow lorises altered their home range use between 2014-2015, we computed the home ranges of the eight focal pairs based on 5851 locations using the 95% minimum convex polygon (MCP). We performed all GIS work using R (R 3.0.2, adehabitatHR package) (R Core Team 2013).

Sleep sites

We defined a bamboo sleep site as the stand of bamboo in which a slow loris social group slept. A single stand can contain over 100 stems or culms of bamboo. During one sleeping period, slow lorises sometimes move from one stem to another, making the stand the unit of analysis. We recorded location of bamboo sleep sites of the eight focal pairs of slow lorises once per week from January 2013 (before the appearance of intensive chayote) to December 2015, georeferencing each site using a handheld GPS unit. To measure sleep site reuse we plotted the points collected during 2013, 2014, and 2015 in ArcGIS version 10.3. We created a 5 m buffer around each point to account for standard GPS error in the area, and then counted each point within overlapping buffers as a single reused sleep site. In June 2016, we returned to the locations of 225 unique bamboo sleep sites; each site revisited fell only in the range of one social pair. In particular, we examined: if the bamboo sleep site still stood in 2016; if yes, had it been cut, including number of whole and cut stems remaining and the number of newly sprouting stems; if no, we recorded what was there instead of the bamboo.

Statistical analysis

Behavioural, sleep site and ranging data did not deviate significantly from a normal distribution. To investigate the influence of the chayote production on slow loris, we tested whether the percentage of chayote frame could explain observed variation in individual home range size. We fitted a multiple linear regression to the data, with the percentage of chayote frame within a home range and the year as the explanatory variables. We conducted the analyses in R. We present descriptive statistics of the characteristics of bamboo sleep sites, reporting the mean and $\pm$ 1 standard deviation, with P set at the 0.05 level.

RESULTS

Farmers' perceptions of slow lorises, pests and crops

In 2011 one out of six informants indicated that slow lorises were allies to farmers as they consumed pest insects, but they mentioned this concept only late in the conversation. In 2013 many more informants (13/16) were aware that slow lorises consumed agricultural pests and they brought up this topic earlier on in the conversation. The situation was similar in 2015 when 15/17 informants mentioned it. Quantitatively, salience, as measured by Smith's *S* of 'slow lorises and pest control' started at a low 0.04 in 2011, and then increased to 0.69 in 2013 and 0.72 in 2015.

The knowledge of the importance of bamboo for slow lorises was high in 2011, with five out of six informants mentioning it. This knowledge remained high in 2013 (14/16) and 2015 (13/17), with some informants mentioning it early on in the conversation and others later on. Quantitatively, Smith's *S* of 'slow lorises and bamboo' was 0.54 in 2011, 0.49 in 2013 and 0.53 in 2015. Chayote as a crop was not significant enough for the informants to mention it in 2011 and 2013. In 2015, all informants mentioned chayote as a crop, two-thirds early on. As such salience of chayote was zero in 2011 and 2013 but Smith's *S* equalled 0.83 in 2015, surpassing that of all the other topics they discussed.

The importance of chayote as a crop led farmers we interviewed to claim that chayote was probably the most important cash crop in the area by December 2015. It then had a market value of Rp 5000-6000 (US$0.35-0.42) per kg. On average five trucks of differing sizes collected chayote daily, with a capacity to carry four to seven metric tonnes per truck. Informants estimated that some 25 t of chayote was produced a day in the wider Cipaganti area, which is larger than the area where we study the slow lorises. While initially chayote farmers organised their business independently, by early 2016 a chayote-growing cooperation was started where 50 of the largest chayote farmers joined forces to share costs, logistics, knowledge and profits.

To create a chayote frame, which in our study area on measures a mean of 1500 m^2, or 0.15 ha, 150 bamboo stems of approximately 2 m tall are required for the main vertical supports and 120 lengths of bamboo measuring 6 m each are needed for the main horizontal supports. Farmers we interviewed reported that up to 30% of the poles need to be replaced every six months, a cost that must be considered when investing in chayote. Three species of bamboo occur frequently in Java, but differ in price according to our interviews, including string bamboo at Rp 5000 (US$0.35) per stem; giant bamboo at Rp 9000 (US$0.64) per stem; and clumping bamboo at Rp 20,000 (US$1.41) per stem. At the beginning of the chayote boom our interviewees reported that they sourced most, if not all, this bamboo locally but by 2015 farmers ordered truckloads of bamboo from the north coast of Central Java (i.e., some 250 km to the east) to meet their demands. Some farmers in our area used more durable concrete poles instead of bamboo ones as a longer-term option, but these are far more costly at Rp 30,000 (US$2.12) for a 2 m length of pole. Using mean figures, the initial investment for a bamboo chayote frame, with labour costs, and plants amounts to some US$500. After four months farmers can harvest the first fruits, and from then on production is more or less continuous. With an annual yield of ~40 t per ha (Morton 1981) the break-even point in terms of financial investment is reached well within the first year.

Chayote in the slow loris landscape

Planting of chayote began in the study area in early 2014 with just a few small frames. By July 2014, many farmers had planted chayote; we recorded 34 chayote frames encompassing an area of 1.6 ha. The numbers increased, with an additional 58 frames encompassing 2.5 ha planted by November 2014. By April 2015 we recorded 145 chayote frames representing a total of 7.2 ha (i.e. 12% of the study area). This represents 2.7% (range 0 -5.6 %) of the social pairs home ranges in 2014 and and 3.9 % (range 0 – 13.0%) in 2015 (Fig. 3).

In 2014, the mean slow loris home range size was 7.1 ha + 2.0. In 2015, the mean was 6.6 ha + 1.2 (Table 1, Fig. 3). Over both years the mean was 7.5 ha + 1.1. Home range size was not affected by the year or percentage of chayote frame ($F_{2,13}$ = 1.75, P = 0.21, n= 16).

Behaviour of slow lorises in chayote

We first recorded use of chayote frames by two social pairs of slow lorises (LU, SI) in June 2014. By October 2014, we had also observed pairs SH and OE using the frames. By June 2015, we had recorded all social pairs regularly using chayote frames; the last pair to use the frames was MA with the first record dating to January 2016. Slow lorises used the frames as if they were a normal bamboo substrate, moving fluidly across the bamboo poles to reach rows of trees on opposite ends of farmers' fields. Chayote frames are very dense and difficult for a human observer to move under, and thus we could only record 211 all occurrences sample points of slow loris behaviour in the chayote. Slow lorises used chayote most frequently for travelling (68%), followed by foraging for or feeding on insects (22%), allogrooming (6%), resting (2%), and other (2%). We could not identify insects to the species level, but noted that slow lorises consumed flying insects that they caught with their hands as well as those that they orally removed from the chayote frames.

Slow loris sleep sites

We recorded the social pairs in a bamboo sleep site a total of 1350 times, comprising 514 unique locations, 211 of which had been reused (2013, n=340 with 95 reused; 2014, n=444 with 53 reused; 2015, n=566 with 89 reused). Slow lorises used three species of bamboo, with 8 sleep sites comprised of clumping bamboo, 52 comprised of giant bamboo, and 454 comprised of string bamboo (Fig. 4). In 2016, we revisited 225 bamboo sleep sites used in the period 2013-2015 comprising a mean of 28±21 bamboo sleep sites unique to each pair (Table 2) and found that 89.3% of sleep sites (n=201) remained and were still being used by slow lorises. 11 sleep sites had been replaced by chayote, 11 were replaced by bare ground, and two had disappeared as a result of landslides. The remaining 201 sleep sites ranged in size from 1 to 101 stems, with a mean of 35.5 ± 24.5 stems per bamboo stand. Only three of these stands remained fully intact, with 198 containing cut stems. The mean number of cut stems per bamboo stand was 19.9 ± 15.8, with the mean number of newly sprouting stems being 7.57 ± 10.9. Social pairs differed in the number of sites destroyed, cut stems, and new sprouting stems (Table 2).

DISCUSSION

Farmers in Cipaganti increasingly recognised the importance of slow lorises in the control of agricultural pests, and chayote became more important over time. In 2015 some 12% of the study area was used to grow chayote and on average 4% of the slow lorises' home range comprised chayote frames. Range size of slow lorises only marginally increased over time and remained stable in terms of their geographic position (i.e. no home range size shifts were recorded). Over time Javan slow lorises started using the chayote frames, mostly for travelling but also for feeding and social interactions. Although cutting for chayote disturbed sleep sites, the fast growing bamboo meant that animals still had more than adequate places to sleep.

Researchers have heralded agroforestry as a positive step towards achieving co-existence between wildlife and farmers. Chayote is as a useful vine in such forests, providing shade for lower strata plants (Clerck and Negreros-Castillo 2000). Humans domesticated chayote centuries ago and worldwide have used it for its economic and cultural value (Lira et al. 2002). Chayote has replaced other more traditional agroforestry practices no longer viable on Java (Iskandar et al. 2016). In Cipaganti, it provides excellent economic services, and requires less intensive farming practices compared to root vegetables, being easy to harvest and not requiring the use of pesticides (Morton, 1981). People introduced chayote into the "traditional bamboo garden" (*kebun tatangkalan*) landscape of Cipaganti, where the crop has partially persisted on the basis of deep cultural affinities to this ancient farming practice (Abdoellah et al. 2015). Together with bamboo and other planted trees, chayote frames and the associated climbers provide a form of living fence or canopy corridor for slow lorises and other wildlife, including rare species such as Javan leopard (*Panthera pardus melas)*, Javan ferret badger (*Melogale orientalis)*, banded linsang (*Prionodon linsang)*, and binturong (*Arctictis binturong)*. Such a system, as opposed to monoculture plantation, seems to allow this mammalian diversity to persist in Cipaganti while providing an excellent economic commodity to local people.

Despite the increase in growth of chayote, farmers we interviewed showed sensitivity towards slow lorises, and did so increasingly over the study. In particular, more farmers recognised the role of slow lorises as pest controls and realised that bamboo species are important plants for slow lorises. Since 2012, we have disseminated information about slow lorises and other native species to farmers through newsletters and other events and by providing classes to their children (Nekaris 2016). We also distributed materials such as leaflets, umbrellas and t-shirts emphasising the role of slow lorises in the ecosystem. Such modes of outreach have proven successful in conservation education and community outreach programmes (Evans et al. 1996, Vaughan et al. 2003, Walter 2009). Indeed, Waylen et al. (2010) suggest that integrating the community into conservation programmes is a key way to change attitudes and allow a conservation project to succeed. Human attitudes towards Javan slow lorises differ in adjacent areas, including an unsustainable pet trade in the species, thus any conservation of them in human-modified landscapes must include a human outreach component (Nijman and Nekaris 2015).

Although chayote frames comprised more than 3% of slow lorises' home ranges, home range sizes of the social pairs remained stable and completely within the agroforest matrix. Chayote frames provided a substrate to move across open fields that had been previously planted with low growing plants treated with pesticides, such as carrots and cassava. Chayote frames appeared to offer the slow lorises a network of substrates that shielded them from predators and contained an abundance of insects. Researchers have previously reported the ability to maintain home ranges completely within for wood mice (*Apodemus sylvaticus)*, golden-headed lion tamarins (*Leontopithecus chrysomelas)* and three-toed sloths (*Bradypus variegatus)* (Vaughan et al. 2007, Oliviera et al. 2011, Rosalino et al. 2011). Wood mice can exploit planted olive groves, and also showed a preference for areas with understory; these preferences were interpreted as improving female fitness and avoiding predators (Rosalino, et al., 2011). Golden-headed lion tamarins and three-toed sloths could survive with their home ranges completely in agroforests (Vaughan et al. 2007, Oliviera et al. 2011). Although tamarin home ranges were smaller than in primary forest, animals were heavier in size and reproduced well. Tamarins relied largely on planted jackfruit (*Artocarpus heterophyllus*). In the case of three-toed sloths, they integrated human-planted living fences into their home ranges. A similar scenario can be observed in Javan slow lorises, whose plant consumption of exudates and nectar is completely from human-introduced species, and whose movements rely heavily on human-planted substrates (Rode-Margono, et al., 2014). Unlike these taxa, however, slow lorises eat mainly gum, insects, and nectar, meaning that resources they consume do not put them in competition with humans, and even have the capacity to help humans.

The chayote bamboo frames provided a new substrate network that slow lorises used for both foraging and moving across their fragmented landscape. Indeed, the full range of behaviours exhibited by slow lorises in chayote in this study mirror the general behavioural ethogram reported Rode-Margono et al., (2014) for the same population (foraging and feeding – 22.4% in this study vs 31% in Rode-Margono, et al., 2014; resting 2%

vs 33%; travelling 68% vs 14%; grooming 6% vs 7%, other 2% vs 13%). The connectivity provided by chayote frames and the high number of insects available due to lack of pesticides can help explain the higher proportion of feeding and travelling. The rapid incorporation of the frames into the slow loris behavioural repertoire is an example of their flexibility and ability to survive in human-modified landscapes, at least for the period of our study. Indeed, slow lorises conform to Nowak and Lee's (2013) statement that the ability to expand niche breadth via resource switching, including substrate choice and modification of diet, is key to withstanding the risks of anthropogenic habitat modification.

The harvesting of the fast-growing bamboo led to the disappearance of some 10% of bamboo sleep sites. Most (98%) of the remaining bamboo sleep sites were affected by the harvesting practises for chayote but enough bamboo stems remained for the slow lorises to keep using bamboo stands as sleep sites. Bamboo is by far the most important sleep site for slow lorises in Cipaganti comprising 96% of all sites observed since 2012 (1st author, unpublished data). Throughout their range, slow lorises never use tree holes and rely on forms of closed substrates for sleeping including dense shrubs, palms, lianas and bamboo stands (Kenyon et al. 2014, Wiens 2002). Pygmy lorises (*N. pygmaeus*) sleep on high clumps of terminal tree branches with a preference for very dense edge forests (Streicher and Nadler 2003). Slow lorises have been never been observed to sleep on the ground and are typically found at 1.8-35.0 m height (Wiens 2002). The maintenance of bamboo shrubs in Cipaganti is clearly vital for their perseverance in this human-dominated landscape, and the current human practice of only cutting parts of bamboo stands is for the time being allowing this persistence.

We agree with Sheil and Meijaard (2010) who describe the 'tainted nature delusion', whereby conservationists neglect the value of human-modified habitats. Researchers in temperate regions have long recognised the value of these ecosystems (Cassano et al. 2014) and it would be prudent for those working in tropical and subtropical regions to follow suit. Studying a difficult to observe, cryptic nocturnal primate like the Javan slow loris in a human-modified landscape has several advantages. While experiencing the effects of rapid environmental change, the Javan slow loris has created an opportunity for researchers to understand their ecological, behavioural, physiological and cognitive capacities (Hockings, et al. 2015). Studying flexibility in these situations may shed light on the evolution and adaptability of extant strepsirrhine and extinct early primates. Species level evolutionary history plays an important role in the response to novel environments (Hendry et al. 2001). An organism's response to human disturbance can be categorized as addressing novel predators, using novel resources, avoiding novel abiotic threats, and acclimating to fluctuating spatiotemporal conditions (Sih et al. 2011). In the case of the Javan slow loris, our findings highlight their behavioural flexibility in a human-modified landscape. Recent IUCN Red List assessments have determined that over 50% of primates face extinction (Estrada, et al. 2017). With the rapid change in habitat transformation for agricultural practices sweeping the tropics, we feel it is urgent to understand the behaviour of primates in such landscapes, and to find ways they can continue to share these spaces with humans.

ACKNOWLEDGEMENTS

We thank the villagers in Cipaganti and other parts of West Java for their time and patience in sharing their views and knowledge unreservedly with us. We thank Indonesia RISTEK and the regional Perhutani and BKSDA for authorizing the study. Amersfoort Zoo, Augsburg Zoo, Brevard Zoo, Cleveland Zoo and Zoo Society, Columbus Zoo, Conservation International Primate Action Fund and Margot Marsh Biodiversity Fund, Cotswolds Wildlife Park, Disney Worldwide Conservation Fund, Henry Doorly Zoo, International Primate Protection League, Little Fireface Project, Longleat Safari and Adventure Park, Mohamed bin al Zayed Species Conservation Fund (152511813), Memphis Zoo, Nacey Maggioncalda Foundation, National Geographic (GEFNE101-13), People's Trust for Endangered Species, Phoenix Zoo, the Royal Geographical Society (with IBG), Shaldon Wildlife Trust, Shepreth Wildlife Park, Sophie Danforth Conservation Biology Fund, Whitley Wildlife Conservation Trust, and ZGAP provided the funding for this project. We thank our field team Y. Nazmi, A. Nunur, D. Rustandi, R. Cibabuddthea, D. Spaan, A. Zaelany, Jessica Wise and Lewis Castle. We thank S. McCabe and R. Sawyer for editorial assistance. We thank two anonymous reviewers and the Associate Editor for extensive comments and the Editor-in-Chief for her help with the submission process.

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Figure Legends

Figure 1. Photographs of chayote frame structure in the Cipaganti area; a.) View from below a fully covered chayote frame; b.) View from above a chayote frame, built as cover, over a farmer's coffee plantation. Photos by Kathleen Reinhardt.

Figure 2. Location of Cipaganti in West Java, Indonesia.

Figure 3. Chayote frames and 95% MCP of Javan slow lorises social pairs (n=8) over the study area in Cipaganti, Java, Indonesia in 2014 and 2015. The names of the social pairs are indicated at the top.

Figure 4. Images of Javan slow lorises in Cipaganti and their bamboo habitats. (A) stand of string bamboo; (B) a close up of a Javan slow loris in string bamboo; and (C) a typical image of a slow loris from a distance in string bamboo as indicated by the arrow.