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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 behavior, home ranges, and sleep sites, we conducted interviews with local farmers and analysed the above variables in relation to chayote expansion between 2011 and 2015. Interviews with farmers in 2011, 2013, and 2015 confirm the importance of chayote and of bamboo and slow lorises in their agricultural practices. 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 to 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,

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Coexistence between Javan Slow Lorises (*Nycticebus javanicus*) and Humans in a Dynamic Agroforestry Landscape in West Java, Indonesia

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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 behavior, home ranges, and sleep sites, we conducted interviews with local farmers and analysed the above variables in relation to chayote expansion between 2011 and 2015. Interviews with farmers in 2011, 2013, and 2015 confirm the importance of chayote and of bamboo and slow lorises in their agricultural practices. 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 to 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.

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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, 2017; Stafford *et al.* 2016). 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 (Cassano *et al.* 2014; Meijaard and Sheil 2008). 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 behavioral 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 be studied only in such contexts (Hockings *et al.* 2015). Increasingly, however, the importance of anthropogenic habitats to primate ecology, conservation, and evolution is 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 crops (Estrada 2006; Williams-Guillén *et al.* 2006). Although such interactions are not always amicable, primates can show remarkable behavioral flexibility, including dietary and habitat switching, and changes in polyspecific interactions (Moore *et al.* 2010; Morrogh-Bernard et al. 2014; Nowak and Lee 2013; Tisovec 2014), 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 in which 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 and 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 (Kumara *et al.*

2016; Nekaris and Rasmussen 2003), Milne-Edward's potto (*Perodicticus edwardsi*) in Cameroon (Pimley *et al.* 2005), and by Dian's tarsier (*Tarsius dianae*) in Sulawesi (Merker *et al.* 2005). /Q4

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 howlers (*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 (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*), and 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 mimics 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 (cf. 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 hypothesized to protect them from extreme temperatures and predators (Nekaris 2014). As slow lorises are territorial, the sleep sites of a 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 reused) as sleep sites daily by slow lorises. Typically, 20–40 bamboo sleep sites are present in each slow loris's home range (K. Nekaris, *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 ca. 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. Owing 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 behavior 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 comprising 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 behavioral 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 2013–2015.

Methods

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

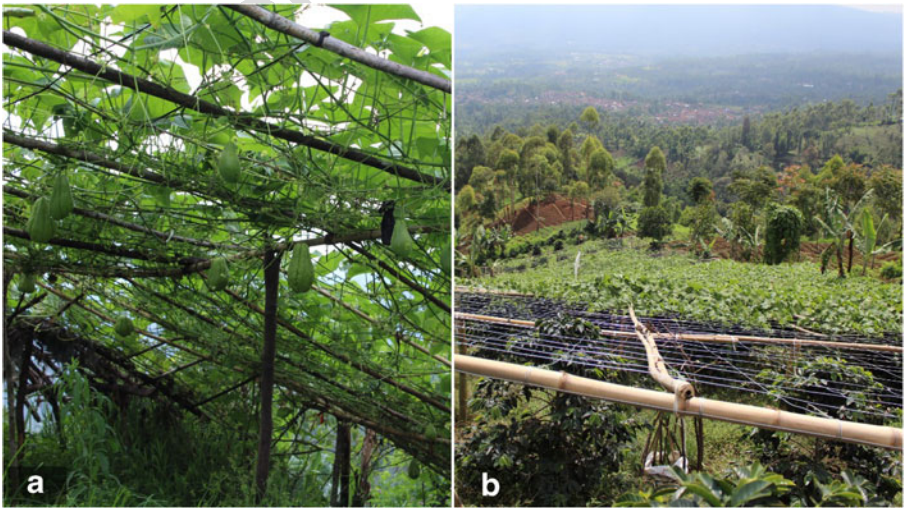

Fig. 1 Photographs of chayote frame structure in the Cipaganti area. **a** View from below a fully covered chayote frame. **b** View from above a chayote frame, built as cover, over a farmer's coffee plantation. Photos by Kathleen Reinhardt.

empowerment (Nekaris 2016). We conducted the study in an area of ca. 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 ca. 3000 people, living at a density of 135 people/km^2 (Nekaris 2016). The village is located at 1345 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 2500 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 (300–2000 m asl) that requires a high relative humidity of around 80–85%, high annual precipitation of ≥1500 without a marked dry season, and 12 h of daylight to initiate flowering. The temperature should be between 13 and 21 °C; temperatures below 13 °C damage small and unripe fruits whereas temperatures above 28 °C lead to excessive growth, loss of flowers, 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 increased from 188 ha in 2012 (22% of the provincial total)

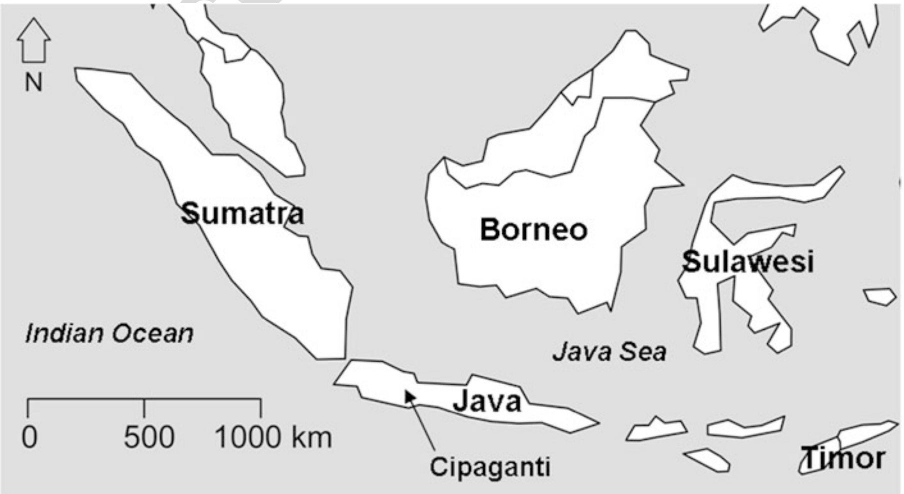

Fig. 2 Location of Cipaganti in West Java, Indonesia.

to 360 ha in 2015 (33% of the provincial total). Production in 2015 was 14,499 t/yr. (cf. 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 be around at least 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 (6 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 focused on the importance of slow lorises to the village, 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 centered 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 on any topic they felt to be relevant, without any constraint placed on 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., whether 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 Behavioral 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 behavior of slow lorises in relation to chayote frames, we analyzed behavioral 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 unimale–unifemale 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 unimale–unifemale social pairs (Table I). After catching the slow lorises by hand, we equipped them with 19-g VHF collars (PIP3, Biotrack, Wareham, UK). With the assistance of local field trackers, we located collared individuals using an antenna (Lintec flexible, Biotrack, Wareham, UK) and a receiver (Sika receiver, Biotrack, Wareham, UK), and recorded their location every 15 min using a handheld GPS unit (GPS62s, Garmin International, Olathe, KS, USA). For direct observations we used head torches (HL17 super spot, Clulite, Petersfield, UK) fitted with a red filter. To observe the behavior of slow lorises in chayote, we followed slow lorises for 3199 h between 17:00 and 05:00 h, from January 2014 to December 2015 (a mean of 13 ± 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) behavioral ethogram. Chayote frames are very dense and often when slow lorises enter these frames they are out of sight until they reemerge into a tree or bamboo. To see if slow lorises altered their home range use between 2014 and 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 >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.

Table I Social pairs of 16 collared Javan slow lorises and associated home range sizes in Cipaganti, West Java, Indonesia from January 2014 to December 2015

Social pair	Adult female/adult male	Home range size 2014 (ha)	Home range size 2015 (ha)	Percentage change
CH	Charlie and Toyib	1.4	2.5	+79
EN	Ena and Rasi	2.6	5.5	+111
LU	Lucu and Pak B	10.4	10.2	–2
MA	Maya and Fernando	6.5	9.9	+52
OE	One Eye and Azka	9.3	8.4	–10
SH	Shirley and Mo	2.2	3.5	+45
SI	Sibau and Damai	18.3	9.8	–46
TE	Tereh and Alomah	10.8	2.7	–75

We estimated home range sizes from 95% minimum convex polygons based on observed locations ($N = 5851$)

Statistical Analysis

Behavioral, 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 ±1 standard deviation, with P set at 0.05.

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 United Kingdom and Commonwealth and that the University Research Ethics Committee of Oxford Brookes University approved.

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* equaled 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 4–7 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. Although initially chayote farmers organized their businesses independently, by early 2016 a chayote-growing cooperation was started in which 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 ca. 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 6 mo, 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 labor costs, and plants amounts to some US$500. After 4 mo farmers can harvest the first fruits, and from then on production is more or less continuous. With an annual yield of ca. 40 t/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 I, 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 ($F_{2,13} = 1.75$, $P = 0.21$, $N = 16$).

Behavior 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 behavior in the chayote. Slow lorises used chayote most frequently for traveling (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 consisting of clumping bamboo, 52 consisting of giant bamboo, and 454 consisting 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 II) and found that 89.3% of sleep sites ($N = 201$) remained and were still being used by slow lorises. Eleven sleep sites had been replaced by chayote, 11 were replaced by bare ground, and 2 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 3 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 II).

Discussion

Farmers in Cipaganti increasingly recognized 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

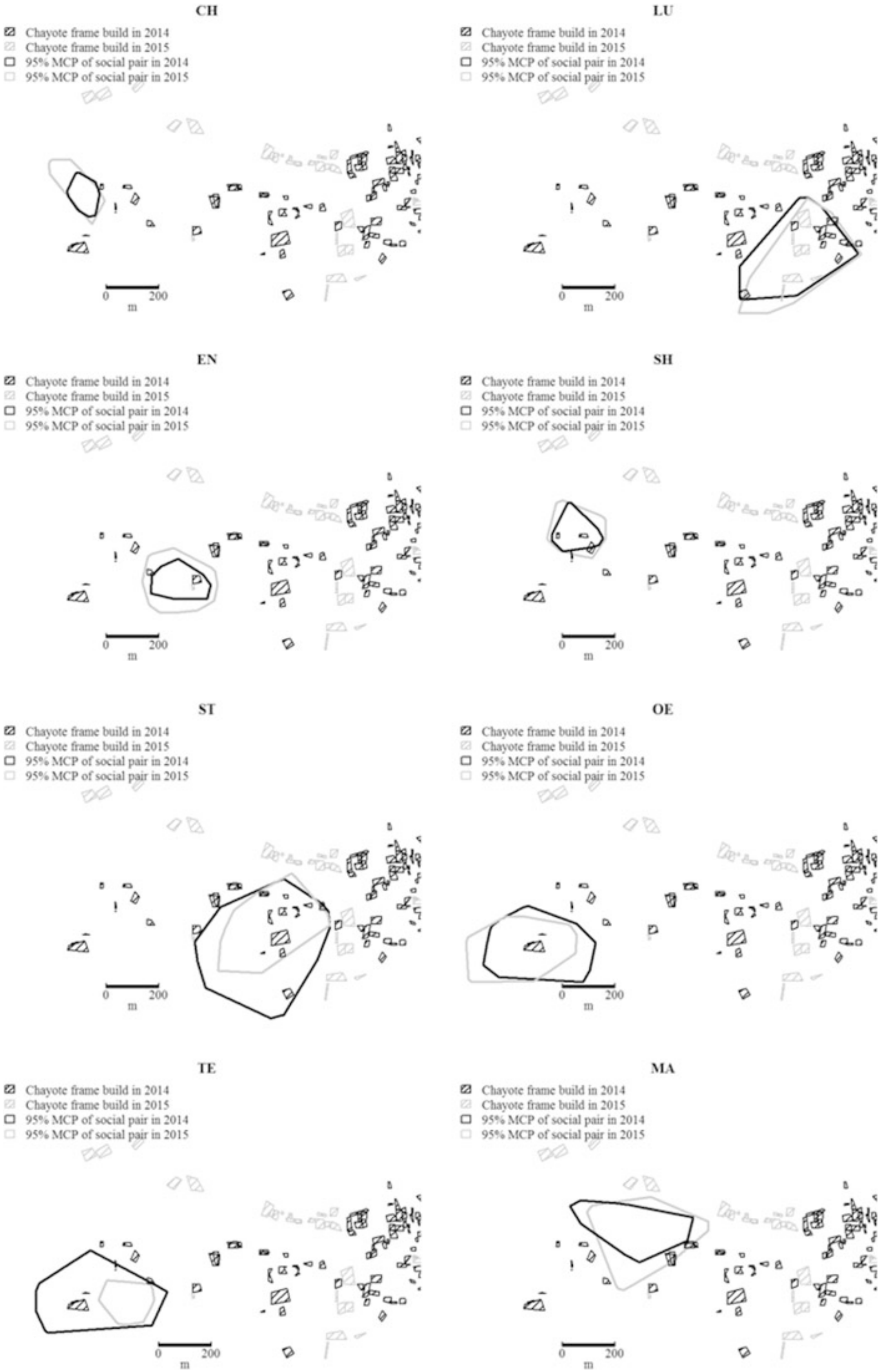

Fig. 3 Chayote frames and 95% MCP of Javan slow lorises social pairs (N = 8) over the study area in Cipaganti, Java, Indonesia in 2014 and 2015. The names of the social pairs are indicated at the top.

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 traveling 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 toward achieving coexistence 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

Fig. 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. **c** A typical image of a slow loris from a distance in string bamboo as indicated by the arrow.

Table II Parameters surrounding bamboo sleep sites for eight Javan slow loris social pairs in Cipaganti, West Java, Indonesia, showing the total number of unique sleep sites, including those revisited in brackets from January 2013 to December 2015, the number of sleep sites we assessed in April 2016, the number of the assessed sites that were destroyed, the altitude of the assessed sleep sites in meters above sea level, and the numbers of cut trunks and new sprouting trunks of the assessed sites

Social pair	Total sites (revisited)	Assessed sleep sites	No. sites destroyed	Altitude (m asl)	Cut trunks	New sprouts
CH	54 (25)	16	2	1495 ± 79.0	27.9 ± 23.7	3.8 ± 4.9
EN	91 (37)	50	10	1421 ± 17.3	18.4 ± 16.2	6.0 ± 4.5
LU	61 (24)	13	1	1396 ± 32.1	17.17 ± 9.0	5.0 ± 3.6
MA	38 (14)	17	1	1420 ± 48.7	22.7 ± 10.0	7.12 ± 6.2
OE	93 (39)	13	1	1456 ± 74.9	17.33 ± 3.9	4.08 ± 3.09
SH	42 (21)	12	1	1454 ± 30.2	25.4 ± 8.2	4.7 ± 3.2
SI	72 (26)	66	6	1401 ± 34.6	16.04 ± 15.3	7.76 ± 8.3
TE	63 (25)	38	2	1452 ± 45.8	19.6 ± 18.9	12.3 ± 21.3
Total	514 (211)	225	24	1428 ± 50.4	19.04 ± 15.9	7.57 ± 10.9

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 toward slow lorises, and did so increasingly over the study. In particular, more farmers recognized the role of slow lorises as pest controls and realized 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, emphasizing the role of slow lorises in the ecosystem. Such modes of outreach have proven successful in conservation education and community outreach programs (Evans *et al.* 1996; Vaughan *et al.* 2003; Walter 2009). Indeed, Waylen *et al.* (2010) suggest that integrating the community into conservation programs is a key way to change attitudes and allow a conservation project to succeed. Human attitudes toward 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 2014).

Although chayote frames comprised >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*) (Oliveira *et al.* 2011; Rosalino *et al.* 2011; Vaughan *et al.* 2007). 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 (Oliveira *et al.* 2011; Vaughan *et al.* 2007). 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 behaviors exhibited by slow lorises in chayote in this study mirror the general behavioral 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%; traveling 68% vs. 14%; grooming 6% vs. 7%; other 2% vs. 13%). The connectivity provided by chayote frames and the high number of insects available because of the absence of pesticides can help explain the higher proportion of feeding and traveling. The rapid incorporation of the frames into the slow loris behavioral 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 practices 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 (K. A. I. Nekaris, *unpubl. 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 (*Nycticebus 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 cutting only parts of bamboo stands is for the time being allowing this persistence.

We agree with Sheil and Meijaard (2010) in their description of the "tainted nature delusion," whereby conservationists neglect the value of human-modified habitats. Researchers in temperate regions have long recognized 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, behavioral, 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.* 2011). 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 behavioral flexibility in a human-modified landscape. Recent IUCN Red List assessments have determined that >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 behavior of primates in such landscapes, and to find ways they can continue to share these spaces with humans.

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AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES.

Q1. Affiliation 1 has been set as the corresponding affiliation, please check if correct.

Q2. The citation “Morrogh-Bernard 2014” has been changed to “Morrogh-Bernard et al., 2014” to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.

Q3. Ref. "Tisovec 2014" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list.

Q4. The citation “Pimley et al. 2006” has been changed to “Pimley et al., 2005” to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.

Q5. The citation “Nijman and Nekaris 2015” has been changed to “Nijman and Nekaris, 2014” to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.

Q6. The citation “Hendry et al. 2001” has been changed to “Hendry et al., 2011” to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.